Population Dynamics Models in Plant–Insect Herbivore–Pesticide Interactions

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Abstract

We consider several population dynamics models in investigating data from controlled experiments with aphids in broccoli patches surrounded by different margin types (bare or weedy ground) and three levels of insecticide spray (no, light, or heavy spray). We carry out parameter estimation computations along with statistical analysis to compare autonomous versus nonautonomous model dynamics. We conclude with a brief discussion of some not-so-subtle pitfalls that can arise when using quantitative measures of model fit-to-data to make biological inferences as well as offer a positive example of how one might combine *a priori* biological hypothesis and intuition with rather sophisticated (from a field biology viewpoint) mathematical methodologies to suggest synergisms.

1 Introduction

Ecologists interested in issues including insect pest control and preservation of rare species study the effects of various types of disturbances on insect populations. Historically, disturbances such as introduction of natural enemies, vegetation diversity, and traditional pesticides have each been considered independently. Often however, introduction of habitat diversity or natural enemies proves inadequate as a single control on insect herbivore populations. Furthermore, risks associated with traditional pesticides often make their use undesirable. We report here on a previous field study that explores the combined effect of vegetation diversity and chemical intervention, and offer new mathematical observations based on its data.

Ecologists have long considered increasing plant diversity to regulate insect herbivore populations in agroecosystems (see, e.g., [4] & [10]). Habitat diversity either entices herbivores to leave the protected area or boosts natural enemy populations in the surrounding area ([16], [22]). These methods are often moderately successful, but their effects are not typically sufficient for pest control ([1], [21]). (For more extensive information on vegetation diversity studies, consult the references in Banks and Stark [6].)

Chemical pesticide application is another long-standing, popular, and often successful single form of population regulation, but broad spectrum pesticides are often criticized for their environmental and public health risks. In response, biorational pesticides that target only certain insect taxa have been developed. The selectivity of these pesticides may be doubly advantageous: they can simultaneously target herbivore pests while leaving natural enemies in the ecosystem intact. This selectivity suggests regulating insect herbivores

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with combinations of pesticide disturbances and biotic factors (including natural enemies and vegetation diversity). Ecologists are optimistic about the success of such combined intervention. In fact, laboratory and field studies by Losey and Denno [15] show that combinations of two or more natural enemies may act synergistically, while other studies suggest additive [8] or sub-additive [17] interactions. The work described in this report is motivated by the hope that the synergy of selective pesticides and natural enemies present in weedy vegetation will reduce insect herbivore populations.

In the summer of 1999, Banks and Stark [6] conducted a full-factorial design field experiment to explore the potentially combined effects of vegetation diversity and selective pesticide disturbance on aphid populations in a broccoli agroecosystem. They applied three concentration levels of the biorational pesticide imidacloprid to broccoli patches surrounded by either bare ground or weedy vegetation.

With the aid of multivariate statistical techniques (MANOVA with General Linear Models), Banks and Stark concluded that aphid populations respond to an interaction between vegetation diversity and pesticide concentration, though it seemed that aphid response depended on the time lapse after pesticide disturbance. They did not consider mathematical models of population dynamics in studying these external influences on aphid populations.

In this paper we describe our efforts fitting population dynamics models to data from the Banks-Stark field study. In particular, we first use ordinary least squares techniques to fit several autonomous ordinary differential equation (ODE) models to each of the six datasets (two margin types each with three pesticide spray levels). Motivated by both varying environmental factors and changes in dynamics due to pesticide application, we also investigate the same set of models with piecewise constant and piecewise linear time-varying coefficients in the corresponding non-autonomous ODEs. Parametrizing these time-varying coefficients introduces additional degrees of freedom, but in general the non-autonomous systems provide substantially better fits to the data. Specifically, chi-squared tests reveal that increasing degrees of freedom to move from constant to time-varying coefficients yields statistically significant improvement in model fit.

For some of the models and datasets considered, we show how to use system sensitivity theory in conjunction with nonlinear regression techniques from statistics to calculate standard errors for estimated parameters. We observe large variance estimates for the parameters, in part due to the large numbers of free parameters considered and relatively small number of data points. We also report on numerical experiments conducted in hopes of further explaining these large variances.

Finally, we examine two of our models that characterize the population dynamics and compare model parameters under various margin types and spray levels. Our ultimate goal here is to understand the influence of natural enemies or other margin-based factors separately from that of the insecticide.

2 Field study methods and data description

Banks and Stark conducted their full-factorial design field experiment during the summer of 1999 at a Washington State University experimental farm in Puyallup, Washington. They established 2.5m square plots each containing 16 broccoli plants and surrounded by 1m wide margins of either weedy vegetation or bare ground. At three points in the growing season, broccoli in each type of margin plot was treated with no pesticide spray, low concentration (15 g ai/ha; active ingredient per hectare) imidacloprid spray, or high concentration (30 g ai/ha) imidacloprid spray. Two replicates of each of the six treatment/margin combinations were placed in each of three fields (blocks) for a total of 36 experimental plots. Thus we have data from six plots for each of the following condition pairs:

1. Bare margin, no spray;
2. Bare margin, low spray (15 g ai/ha);
3. Bare margin, high spray (30 g ai/ha);
4. Weedy margin, no spray;

5. Weedy margin, low spray (15 g ai/ha); and
6. Weedy margin, high spray (30 g ai/ha).

Unwanted weedy vegetation was regularly removed by a combination of tractor and hand cultivation. Plots were watered regularly throughout the growing season and dead or missing plants were replaced by similar sized plants as needed. The study commenced with transplantation in late June; pesticide spraying began in late July; and the study concluded in September. Imidacloprid spray was applied on July 23, August 13, and August 27, denoted by days 0, 21, and 35, respectively, in this paper.

At 4, 7, and 10 days after each pesticide spray (a total of 9 censuses), Banks and Stark randomly selected a subset of 8 plants in each plot and visually censused the aphids. They counted all aphids on both sides of broccoli leaves and all other surfaces. Average cylindrical plant volume in each plot was obtained mid-season by measuring broccoli plant dimensions. Herbivore response to treatment manipulations was then calculated by dividing the number of aphids on a plant by the mean plant volume for that plot. Thus the census and volumetric measurements combined to yield a measure of aphid density (aphids per cubic meter) for each plot. In both Banks and Stark [6] and our present effort, inter-block variability was reduced by averaging the data across the six plots of each type (i.e., across three blocks, each with two replicates) to obtain a mean measure of aphid density over time. We fit our ODE models to this mean density data.

The datasets can be viewed in Section 5.

3 Mathematical models

For this study, we consider several ordinary differential equation models of population dynamics. The models each involve a single state variable $N(t)$, which denotes the aphid population density: (mean aphids)/m^3. The models all have the general form

$$\frac{dN(t)}{dt}(t)\left(=\dot{N}(t)\right) = B(N(t),t)\,N(t) - D(N(t),t)\,N(t), \tag{M}$$

where $\frac{dN}{dt}$ (equivalently $\dot{N}$) denotes the time derivative of the state variable $N(t)$; B, a (potentially time- and/or state-dependent) birth rate; and D, a (potentially time- and/or state-dependent) death rate. Note that for Model 3 below we will let $a = b - d$ denote a combined birth/death rate, when $B = b$ and $D = d$.

The models used in our study (omitting the implicit time dependence of N and $\dot{N}$) are listed here.

1. Model 1 is the standard exponential model for birth. Here $B = b(t) > 0$ and $D = 0$ in (M) above. The resulting ODE is
$$\dot{N} = b(t)N. \tag{1}$$
Because aphids reproduce by parthenogenesis (i.e., asexually) in the field, exponential growth is a reasonable assumption for their population dynamics, especially when densities are below the carrying capacity.

2. Model 2 is the standard exponential model for death. Here $B = 0$ and $D = d(t) > 0$ in (M) above, resulting in
$$\dot{N} = -d(t)N. \tag{2}$$
This model assumes mortality due to pesticides and/or predation is the driving force behind aphid population dynamics.

3. Model 3 is the standard exponential model for population dynamics, allowing for simultaneous exponential birth and death. Here $B = b(t) > 0$ and $D = d(t) > 0$ in (M) above and we have
$$\dot{N} = b(t)N - d(t)N = a(t)N. \tag{3}$$

4. Model 4 is similar to the exponential death model, but has a density-dependent birth rate that decreases as the population increases. Here $B = \frac{b(t)}{N(t)}$, with $b(t) > 0$ and $D = d(t) > 0$ in (M) above, resulting in
$$\dot{N} = b(t) - d(t)N. \tag{4}$$

5. Model 5 is similar to the exponential birth model, but has a density-dependent death rate that decreases as the population increases. Here $B = b(t) > 0$ and $D = \frac{d(t)}{N(t)}$, with $d(t) > 0$ in (M) above, yielding
$$\dot{N} = b(t)N - d(t). \tag{5}$$

6. Model 6 is the standard logistic model for population dynamics (Verhulst equation), which incorporates a carrying capacity. Here $B = b(t) > 0$ and $D = d(t)N(t)$, with $d(t) > 0$ in (M) above, so we have
$$\dot{N} = b(t)N - d(t)N^2. \tag{6}$$

7. Finally, Model 7 is obtained from the negative of the logistic model, and thus has a threshold rather than a carrying capacity. Here $B = b(t)N(t)$, with $b(t) > 0$ and $D = d(t) > 0$ in (M) above. The resulting model is
$$\dot{N} = b(t)N^2 - d(t)N. \tag{7}$$

   Model 7 embodies the idea that above a population threshold, aphid populations grow exponentially, and below the threshold populations decline to extinction. Since aphids feed by inserting their proboscis into highly pressurized plant phloem, feeding and subsequent growth is facilitated by higher densities of aphids feeding on plants. At lower densities, aphids have more difficulty overcoming plant phloem pressure, which could lead to population decay and extinction, especially when they are vulnerable to predation, pesticide sprays, etc.

The models above are shown with potentially time-varying parameters. In the constant coefficient case, the parameters $B(N(t), t)$ and $D(N(t), t)$, do not explicitly depend on t and thus depend at most on $N(t)$. The constant coefficient models are recovered by making the coefficients $b, d,$ and a constant in the above ODEs. For more information on Models 6 and 7, see Boyce and DiPrima [7]. Note that in each case, a solution to the ordinary differential equation is uniquely determined by imposing a single initial condition, denoted $N_0 = N(t_0)$, where $t_0 = 0$ is the initial time considered in our study.

We first fit the models with constant coefficients (a, b, d) to the data, and then repeat, allowing one time-varying coefficient (one of $a(t), b(t), d(t)$). For models with two parameters, we treat one parameter as constant in time while allowing the other to be time-varying and then do the opposite. In the time-varying cases, we first employ piecewise constant and then piecewise linear coefficients. Figure 1 depicts a sample of the time varying coefficients considered.

For the piecewise constant case, the coefficient is constant a_i on each time interval $I_i, i = 1 \ldots 3$, where I_i denotes the time interval after the i^{th} spray and before the $(i + 1)^{\text{th}}$ (or the end of the study in the case $i = 3$). Therefore in going from constant coefficients to piecewise constant coefficients we add two degrees of freedom to the parameter set (from a single coefficient a to $a_1, a_2,$ and a_3, e.g.). The time-varying coefficient is thus parametrized by a_1, a_2, a_3:
$$a(t) = \sum_{i=1}^{3} a_i \chi_{I_i}(t), \tag{8}$$
where $\chi_{I_i}(t)$ is the characteristic function which has value 1 on interval I_i and 0 elsewhere.

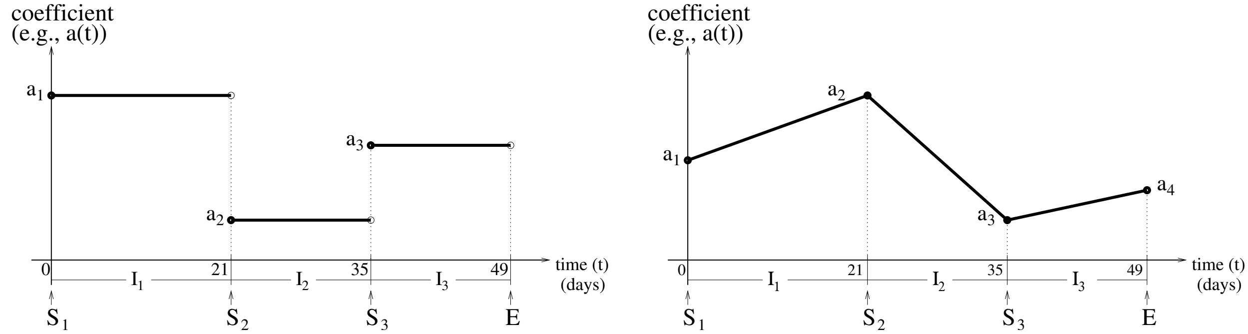

Figure 1: Example of time-varying coefficients. Left plot: piecewise constant, values a_i are on intervals; right plot: piecewise linear, values a_i are at nodes. **S** denotes spray application and **E** denotes end of study.

For the piecewise linear case, the coefficient is linear on each time interval $I_i, i = 1 \ldots 3$, where I_i is as above. The piecewise linear time-varying coefficient can be parametrized by $a_1, a_2, a_3,$ and a_4, the nodal values of $a(t)$ at the three sprays and the final time, respectively. Therefore

$$a(t) = \sum_{i=1}^{4} a_i \phi_i(t), \tag{9}$$

where $\phi_i(t)$ is the i^{th} standard linear 'hat' spline basis function as shown in Figure 2. Hence in changing from constant coefficients to piecewise linear coefficients we add three degrees of freedom to the parameter set (from a single coefficient d to $d_1, d_2, d_3,$ and d_4, e.g.).

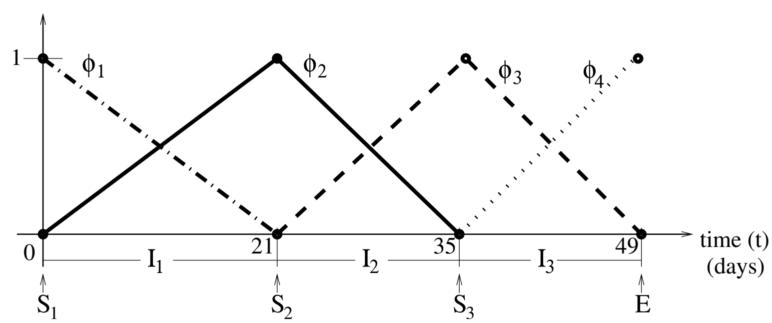

Figure 2: Linear spline basis elements ('hat' functions). $\phi_i(t)$ has value 1 at node i ($\{S_i\}_{i=1}^{3}$ or E) and 0 at other nodes. **S** denotes spray application and **E** denotes the end of the study.

We expect better model fit (smaller residuals and better visual fit) using the non-autonomous models, due to the larger number of degrees of freedom. Certainly the residuals will be at least as small with time-varying coefficients as with constant coefficients. We use statistical analysis to determine whether any improvement in fit is strictly due to the increased degrees of freedom, or is statistically significant given the increase in degrees of freedom.

According to an *in vitro* study, application of imidacloprid selective pesticide affects both insect death and birth rates [18]. However, few studies have been conducted on the sub-lethal effects of selective pesticides (but see [19] and [20]). In addition, the pesticide used is most likely not detected by the aphids prior to ingestion, so any change in death rates incurred after spraying is likely attributable to ingestion of the poison and/or predation, rather than immigration into or emigration from the plot.

The relatively sudden injection of pesticide spray into the environment suggests consideration of piecewise constant rates, though such discontinuous rates may be more characteristic of traditional, broad spec-

trum pesticides. Selective pesticides like the imidacloprid used in this study take longer to build up in the system (they are slowly absorbed into the plant and then ingested by aphids), suggesting that smoother piecewise linear rates may be more sensible. Piecewise linear rates are also more useful for modeling slow changes in the environment. In the case of the Banks-Stark study, declining mean temperatures throughout the study are most likely the principal source of such environmental variation.

From a Stark *in vitro* study [unpublished data], we calculate the following estimates of instantaneous natural birth and death rates (i.e., the coefficients in the model $\dot{N} = (b - d)N$) for two species of aphid commonly observed in the field: *Myzus persicae* and *Brevicoryne brassicae*. In gathering the data reported on in this paper, Banks and Stark observed greater abundance of *M. persicae* (green peach aphid). These rates, given in Table 1, will be used later for comparison purposes.

species	birth rate b	death rate d
M. persicae	0.209869565	0.001059425
B. brassicae	0.250791904	0.001843502
mean	**0.230330735**	**0.001451464**

Table 1: Empirical *in vitro* instantaneous birth and death rates for two species of aphid commonly observed during the field study.

4 Parameter estimation and statistical techniques

4.1 Least squares problem formulation and solution

As stated above, the unique solution of each ODE model depends on an initial condition N_0. Since we do not wish to give considerably more weight to the first observation, we allow the initial condition N_0 to be a free parameter (to be estimated) at time $t_0 = 0$ days. We therefore have the following times and events in our experiment. The event 'S' denotes spray and 'C', collection of census data. Observations are denoted by N_i at time t_i days.

time (days)	0	4	7	10	21	25	28	31	35	39	42	45
event	S	C	C	C	S	C	C	C	S	C	C	C
I.C. or obs.	N_0	N_1	N_2	N_3		N_4	N_5	N_6		N_7	N_8	N_9

We fit each of the models described in Section 3 to each of the six datasets, using an ordinary least squares cost functional to measure model fit to data. The ordinary least squares inverse problem can be stated as follows.

Let q denote the vector of parameters in the model considered, e.g., $q = [b, d, N_0]$ for constant rates or $q = [b, d_1, d_2, d_3, N_0]$ for piecewise constant time-varying rates as described in Section 3. Then the cost function $J(q)$ is given by

$$J(q) = \sum_{i=1}^{9} \left(N(t_i; q) - N_i\right)^2, \tag{10}$$

where $N(t_i; q)$ and N_i denote the model solution (dependent on the choice of parameters) and observation at time t_i, respectively. Consequently, the inverse problem consists of minimizing the function $J(q)$ over the space of admissible parameters $q \in \mathcal{Q}_{ad}$ and thus finding the best model fit to the data. For most of the models, we would ideally take $\mathcal{Q}_{ad}$ to be the entire positive half-space, but in several cases we reduce the parameter space to some subset of $\mathbb{R}^{p+}$, where p is the dimension of the parameter space (length of q) to

make computation feasible. Specifically we impose lower and upper bound constraints l and u on some of the components of q: $l_i \leq q_i \leq u_i$.

When fitting the models with constant or piecewise constant coefficients, the availability of closed form analytical ODE solutions makes computation considerably faster. Employing piecewise linear coefficients prohibits straightforward analytical solution, so we solve the ODEs by invoking the Matlab ODE solver *ode45*, an adaptive explicit Runge-Kutta solver.

We minimize the cost function (10) with a combination of sampling and gradient-based methods. We first apply the *gblSolve* code which is freely available for educational use with Matlab and is also part of the commercial package TOMLAB [13]. This code employs a sampling-based algorithm for global optimization with bound constraints and is based on the DIRECT algorithm [14]. The resulting minimizer from *gblSolve* serves as one of several initial iterates for the bound constraint least squares optimizer, Matlab's *lsqnonlin*, which refines the choice of optimal parameters. The algorithm *lsqnonlin* is a Gauss-Newton method which switches to Levenberg-Marquardt when parameter step sizes are small.

The increased number of degrees of freedom in the models with time-varying coefficients make them more difficult to fit. However, the optimal coefficients from the constant coefficient case and the results of the sampling algorithm prove good initial iterates for the least squares optimization to find piecewise defined coefficients in nearly all cases. We note that the optimal parameters reported in the next section are not unique, but in many cases at least provide good fit to data and reasonable residuals.

4.2 Statistical significance testing

We test the significance of adding additional degrees of freedom to the inverse problem, i.e., using piecewise constant ($s = 2$ additional degrees of freedom) or piecewise linear ($s = 3$ additional degrees of freedom) coefficients, by comparing the cost function values at optimal parameters for constant coefficients (J_{cons}) and those using piecewise coefficients (J_{pw}). For each model we compare the improvement in using the piecewise constant (pwc) or piecewise linear (pwl) coefficient (non-autonomous) model over the corresponding autonomous model. In particular, we use the test statistic

$$U_n = \frac{n\left[J_{cons}(q^*_{cons}) - J_{pw}(q^*_{pw})\right]}{J_{pw}(q^*_{pw})}, \tag{11}$$

where $n = 9$ data points, and q^*_{cons} and q^*_{pw} denote optimal parameters for the two cases, in a χ^2 test with the null hypothesis that constant coefficients are sufficient to fit the data. By computing the tail probability α beyond U_9 in a $\chi^2(s)$ distribution (s denotes number of additional degrees of freedom), we determine the maximum level of confidence $P = (1 - \alpha)$ at which we can reject the null hypothesis. This allows us in many cases to suggest with confidence that the improvement in model fit achieved with time-varying coefficients is significant. Banks and Fitzpatrick developed theoretical foundations for and applied this method to similar problems in 1990 [2] and additional examples can be found in [3].

4.3 Standard error analysis

Any estimate of model parameters from data should be accompanied by an estimate of uncertainty. We illustrate one approach to estimating variance with two of the models under investigation here. For Models 3 and 6 (with constant and piecewise linear coefficients), we assess the variance in the estimated model parameters q^* by employing sensitivity equations to compute standard errors.

To perform this analysis, we first compute the sensitivity of the ODE model solution (denoted by $y = N(t; q)$) to the estimated parameters $q \in \mathbb{R}^p$. Letting $f(t, y; q)$ denote the right side of the ODE and $y_0 = y(0)$ the initial condition at time $t = 0$, we can write the model as

$$\begin{aligned} \dot{y}(t) &= f(t, y; q) && (12)\\ y(0) &= y_0. && (13)\end{aligned}$$

Since we parametrize any time-varying coefficients, we can formally differentiate (12) and (13) with respect to q and interchange the order of the time and parameter derivatives as outlined in [11] and [12]. We thus obtain a p-dimensional system of differential equations for the sensitivities $y_q(t; q)$:

$$\frac{d}{dt}\left(\frac{\partial y(t)}{\partial q}\right) = \frac{\partial f}{\partial y}\frac{\partial y(t)}{\partial q} + \frac{\partial f}{\partial q} \tag{14}$$

with initial condition

$$\frac{\partial y(t)}{\partial q}(0) = \frac{\partial y_0}{\partial q}, \tag{15}$$

which has components either 0 or 1, depending on whether the derivative is with respect to a model parameter or initial condition, respectively.

To solve for $y_q(t; q)$, we augment the original differential equation model with the sensitivity equation system (14) to obtain a $(p+1)$-dimensional system which we solve forward in time. For these computations we utilize the Matlab stiff ODE solver *ode15s*. Coupling the original ODE model and sensitivity equations in this manner ensures that the solution data for $y(t)$ is sufficiently accurate to solve the sensitivity system to the desired accuracy.

EXAMPLE: Consider Model 6 with piecewise linear coefficient $b(t)$. In this case, the ODE model is

$$\begin{aligned} \dot{y}(t) &= \left(\sum_{i=1}^{4} b_i\phi_i(t)\right) y(t) - d\, y(t)^2\\ y(0) &= y_0.\end{aligned}$$

with parameters $q = [b_1, b_2, b_3, b_4, d, y_0]$ ($p = 6$). The augmented ODE (sensitivity) system in this case is

$$\frac{d}{dt}\left[\begin{array}{c} y(t) \\ \hline \left[\begin{array}{c} \cdot \\ \cdot \\ \left[\frac{\partial y(t)}{\partial q}\right] \\ \cdot \\ \cdot \end{array}\right]\end{array}\right] = \left[\begin{array}{c} b(t)y(t) - dy(t)^2 \\ \hline (b(t) - 2dy(t))\left[\begin{array}{c} \cdot \\ \cdot \\ \left[\frac{\partial y(t)}{\partial q}\right] \\ \cdot \\ \cdot \end{array}\right] + \left[\begin{array}{c} y(t)\phi_1(t) \\ y(t)\phi_2(t) \\ y(t)\phi_3(t) \\ y(t)\phi_4(t) \\ -y(t)^2 \\ 0 \end{array}\right]\end{array}\right]$$

with initial condition

$$\left[\begin{array}{c} y(0) \\ \hline \cdot \\ \cdot \\ \left[\frac{\partial y(0)}{\partial q}\right] \\ \cdot \\ \cdot \end{array}\right] = \left[\begin{array}{c} y_0 \\ \hline 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \end{array}\right].$$

We compute the sensitivities $y_q(t;q)$ at the observation times $t = t_i, i = 1 \ldots 9$, using for q the estimated parameter vector $\hat{q} = q^*$, which is considered our best estimate for the true parameters, and form the $9 \times p$ sensitivity matrix

$$Y_q(q) = \begin{pmatrix} y_q^T(t_1;q) \\ \vdots \\ y_q^T(t_9;q) \end{pmatrix}. \tag{16}$$

Under the standard assumptions of classical nonlinear regression theory, together with the assumption that measurement process errors ϵ_i are independently distributed and have constant variance σ^2 (specifically $\epsilon_i \sim \mathcal{N}(0,\sigma^2)$ where ϵ_i is the difference between observation and model at time t_i), we expect the OLS estimate $\hat{q} = q^*$ to be approximately normally distributed (at least asymptotically). Specifically, for large samples,

$$\hat{q} = q^* \sim \mathcal{N}\left[q_0, \sigma^2 \left\{Y_q^T(q_0)Y_q(q_0)\right\}^{-1}\right], \tag{17}$$

where q_0 is the true vector of parameters and $\sigma^2 \left\{Y_q^T(q_0)Y_q(q_0)\right\}^{-1}$, the true covariance matrix (see [9], Chapter 2).

Having no better approximation to the true values q_0 and σ^2 available, we follow standard statistical practice and substitute the computed estimate q^* for q_0 and approximate σ^2 by

$$\hat{\sigma}^2 = \frac{1}{9-p}\sum_{j=1}^{9}\left(y(t_j;q^*) - y_j\right)^2,$$

in (17) to obtain standard errors for our estimates. In particular if

$$C = \hat{\sigma}^2 \left\{Y_q^T(q^*)Y_q(q^*)\right\}^{-1}$$

from (17) above (taken with the described substitutions), we take $\sqrt{C_{kk}}$, to get the standard error for parameter component q_k.

5 Model fitting results

In this section we present a rather exhaustive set of results from our model fitting. Each dataset (corresponding to a particular margin and spray combination) appears in its own subsection, wherein the following appear in order:

1. A table summarizing the optimal parameters, cost, and test statistics for constant and piecewise constant parameters (top) and constant and piecewise linear parameters (bottom). Note that for simplicity in the tables, rows corresponding to b also contain the data for the parameter a for Model 3. Note also that we do not fit the negative logistic model (Model 7) for the case of piecewise linear coefficients, since for this particular model, the optimizer often strays into a part of parameter space where numerical ODE solution fails (specifically, the solution diverges to infinity).

2. Three figures showing the fits for (a) Models 1–3, (b) Models 4 and 5, and (c) Models 6 and 7 with constant and piecewise constant coefficients.

3. Three figures showing the fits for (a) Models 1–3, (b) Models 4 and 5, and (c) Model 6 with constant and piecewise linear coefficients.

4. A summary table for the dataset, showing the cost function values and resulting test statistics.

5. Some comments on the model fits to data for the dataset at hand.

In studying these results, recall that in the time-varying case for models with two coefficients, only one coefficient was taken to be time-varying and the other was held fixed (constant). Also, note that each graph showing the optimal model fit to data includes the corresponding cost function value (J) at the optimal parameters as part of the title.

5.1 Dataset 1: Bare margin, no spray

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	$b \mid a$	1.8256e-12	n/a	-1.1919e-02	3.9127e-07	5.6894e-02	2.1262e-09	2.6150e-04
	d	n/a	1.1919e-02	n/a	1.1919e-02	2.1662e+01	3.6905e-05	9.5972e-02
	N_0	295	395	395	395	366	396	363
	J	5.2730e+04	2.6554e+04	2.6554e+04	2.6554e+04	2.0647e+04	2.8331e+04	1.9926e+04
pwc $b(t)$ or $a(t)$	$b_1 \mid a_1$	9.1295e-14	n/a	1.6415e-02	8.2687e+01	4.8078e-02	2.2503e-01	2.7031e-04
	$b_2 \mid a_2$	9.1315e-14		-5.0672e-02	4.2202e+01	3.5589e-09	1.0400e-01	1.9307e-04
	$b_3 \mid a_3$	9.1279e-14		-4.1650e-03	3.4377e+01	6.2495e-02	8.1183e-02	3.9948e-04
	d	n/a		n/a	1.7606e-01	1.4081e+01	4.6123e-04	9.7158e-02
	N_0	295		316	122	337	187	362
	J	5.2730e+04		1.5651e+04	1.1602e+04	1.6825e+04	1.1092e+04	1.7942e+04
	U	0.00		6.27	11.60	2.04	13.99	1.00
	$1-\alpha$	0.000		0.956	0.997	0.640	0.999	0.392
pwc $d(t)$	b	n/a	n/a	n/a	6.4407e+01	1.0924e-02	1.7696e-01	3.4367e-05
	d_1		3.0316e-14		1.2438e-01	9.7131e-07	3.2862e-04	1.1374e-06
	d_2		2.5052e-02		2.4689e-01	1.7568e+01	6.8698e-04	5.7943e-02
	d_3		2.3795e-02		3.1159e-01	2.6752e+00	8.9685e-04	1.3286e-02
	N_0		363		156	328	203	328
	J		1.8592e+04		1.1621e+04	1.6343e+04	1.0974e+04	1.6093e+04
	U		3.85		11.56	2.37	14.23	2.14
	$1-\alpha$		0.854		0.997	0.694	0.999	0.658
cons	$b \mid a$	7.1900e-12	n/a	-1.1919e-02	4.5435e-05	5.7187e-02	4.8430e-07	–
	d	n/a	1.1920e-02	n/a	1.1927e-02	2.1754e+01	3.6550e-05	
	N_0	295	395	395	395	366	394	
	J	5.2730e+04	2.6554e+04	2.6554e+04	2.6554e+04	2.0647e+04	2.8333e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	3.6050e-13	n/a	1.1232e-01	4.9765e+01	1.8276e-01	1.5264e-01	–
	$b_2 \mid a_2$	3.5950e-13		-4.3865e-02	1.4570e-03	7.7092e-05	1.1703e-02	
	$b_3 \mid a_3$	3.5962e-13		-2.8820e-02	9.9709e-01	6.5141e-02	2.2547e-04	
	$b_4 \mid a_4$	3.6058e-13		7.4932e-03	9.4029e+00	1.2153e-01	2.9598e-02	
	d	n/a		n/a	3.5115e-02	2.2113e+01	1.2550e-04	
	N_0	295		199	145	216	189	
	J	5.2730e+04		1.0123e+04	1.0514e+04	1.0054e+04	1.0193e+04	
	U	0.00		14.61	13.73	9.48	16.02	
	$1-\alpha$	0.000		0.998	0.997	0.976	0.999	
pwl $d(t)$	b	n/a	n/a	n/a	3.4244e+01	1.0776e-01	1.1665e-01	–
	d_1		4.3499e-13		2.6731e-07	9.4160e-01	4.0952e-07	
	d_2		3.7702e-03		1.1831e-01	6.2967e+01	3.8839e-04	
	d_3		3.8183e-02		1.6982e-01	3.0803e+01	5.8297e-04	
	d_4		1.7291e-11		1.7614e-01	1.9366e+01	6.4757e-04	
	N_0		359		172	220	184	
	J		1.8780e+04		1.0497e+04	1.0641e+04	1.0220e+04	
	U		3.73		13.77	8.46	15.95	
	$1-\alpha$		0.707		0.997	0.963	0.999	

Table 2: Bare margin, no spray: Optimal parameters and cost for constant versus piecewise constant coefficients for all models (top) and constant versus piecewise linear coefficients (bottom) for Models 1–6.

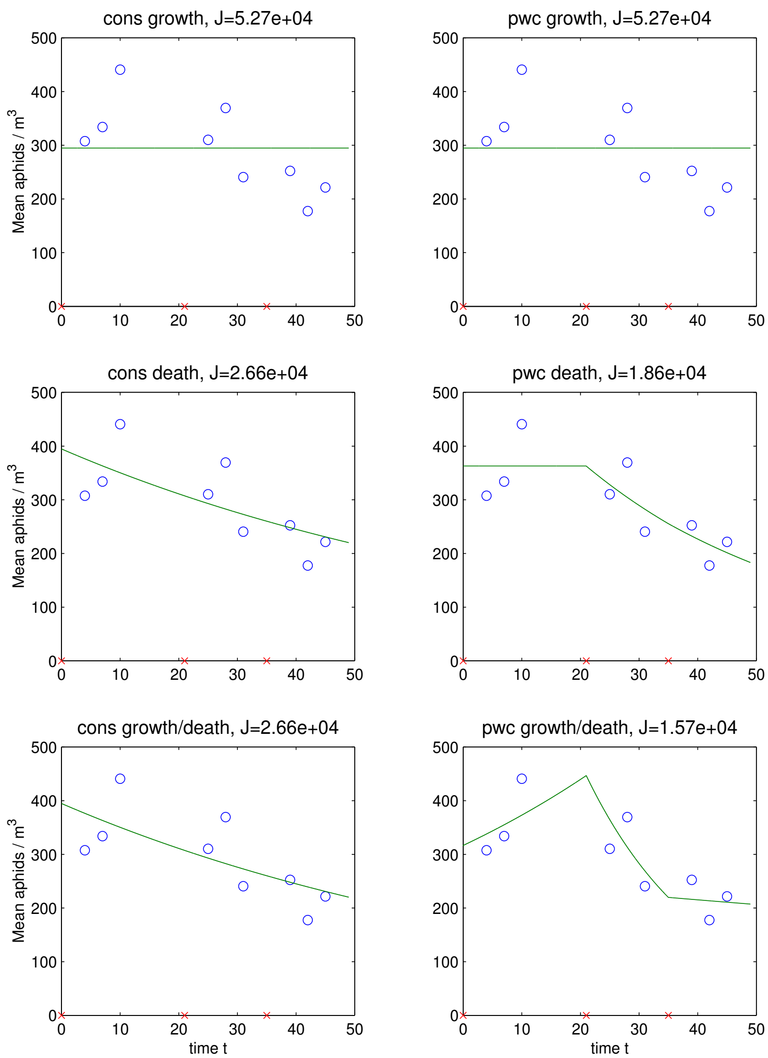

Figure 3: Fit of **exponential models** to data from **bare margin, no spray**. Coefficients are either constant (left column) or **piecewise constant** (right column). Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

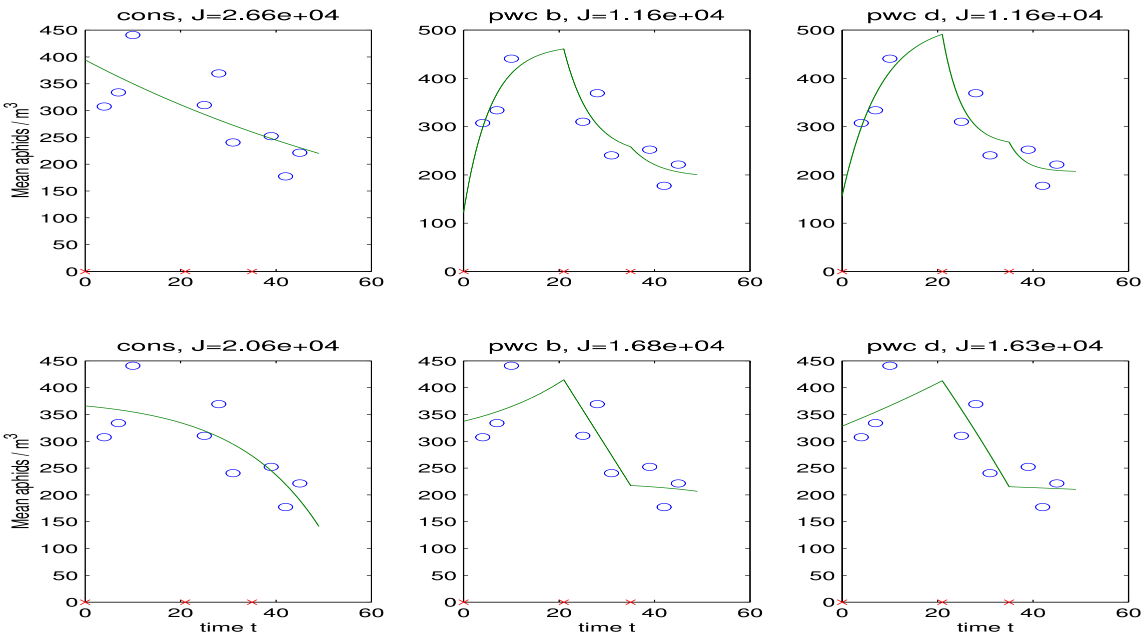

Figure 4: Fit of **Models 4 and 5** to data from **bare margin, no spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, again with results for constant and **piecewise constant** coefficients.

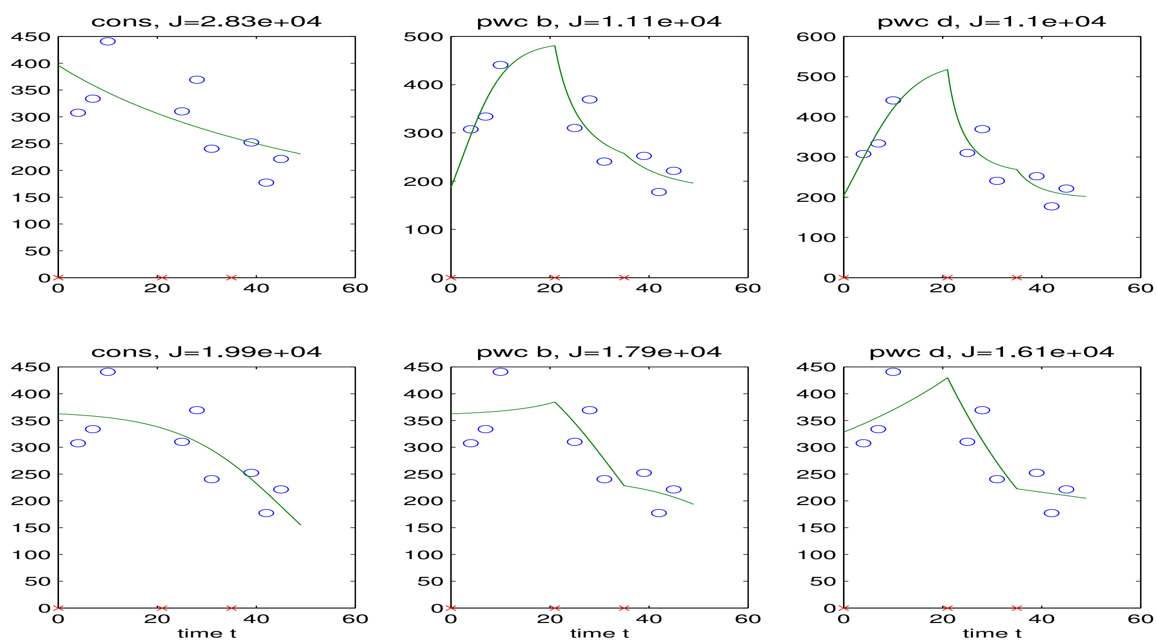

Figure 5: Fit of **logistic Models 6 and 7** to data from **bare margin, no spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN^2 - dN$, again with results for constant coefficients and **piecewise constant** coefficients.

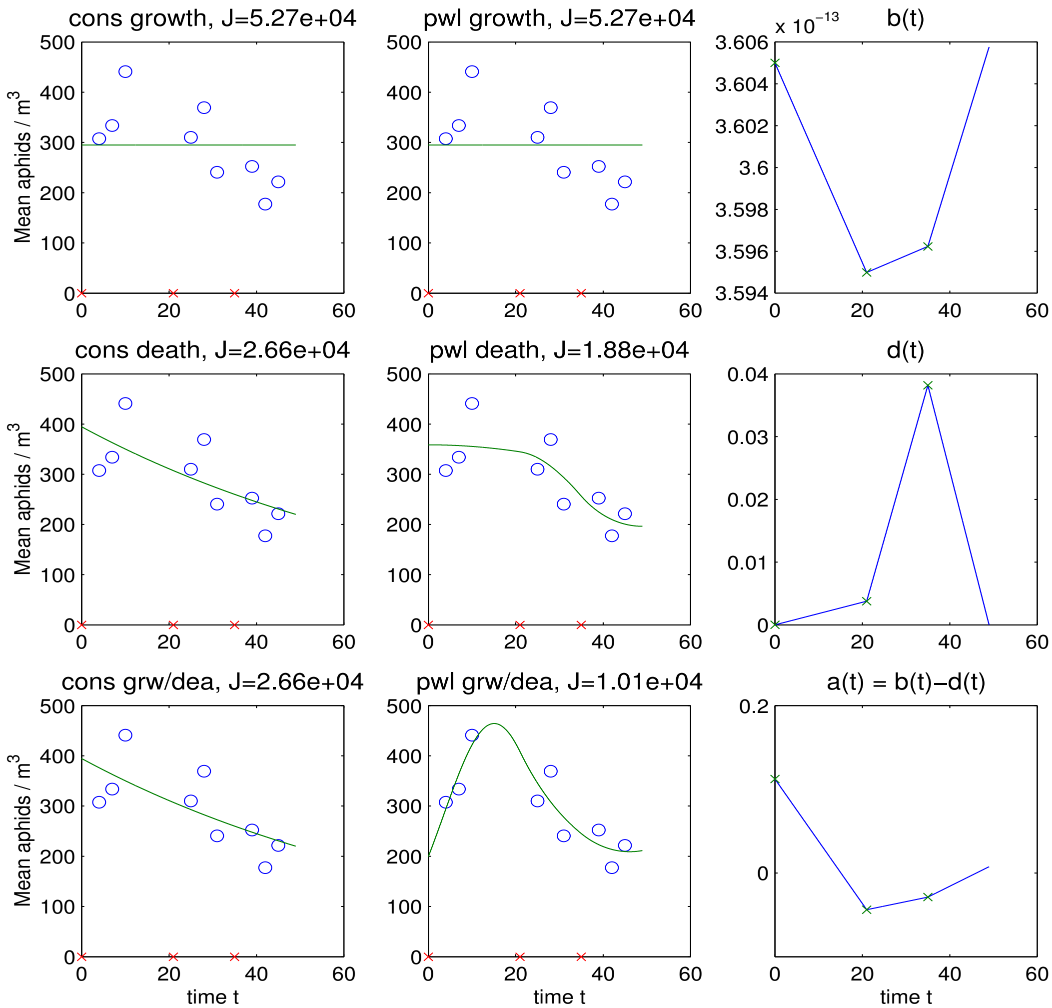

Figure 6: Fit of **exponential models** to data from **bare margin, no spray**. Coefficients are either constant (left column) or **piecewise linear** (center column) and pwl coefficients are shown in the right column. Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

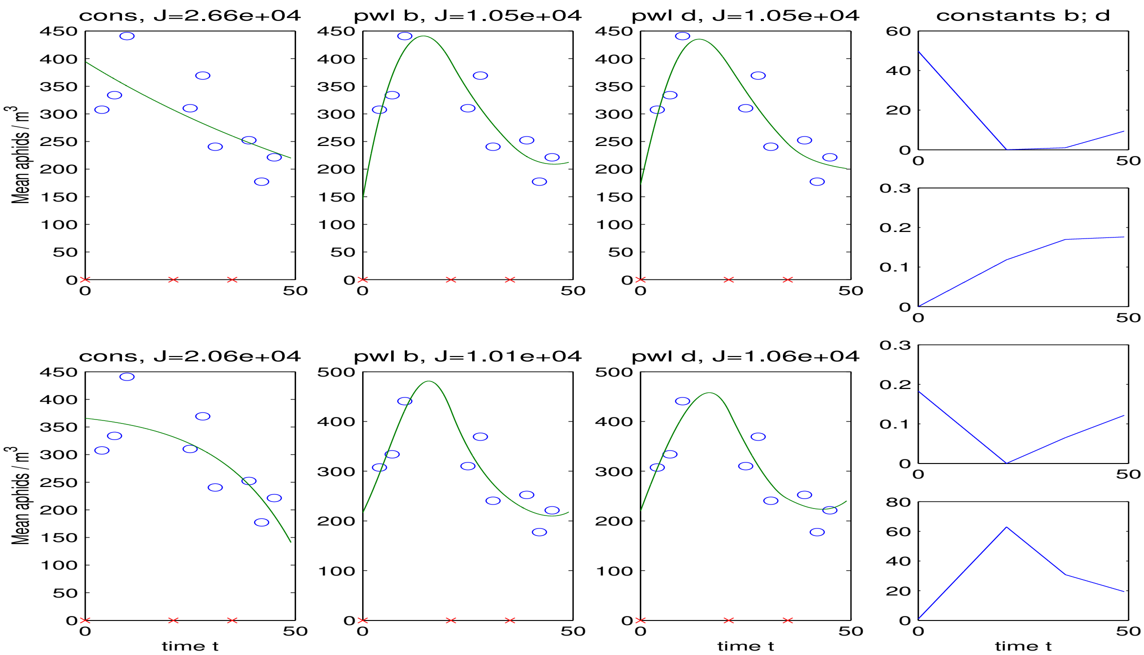

Figure 7: Fit of **Models 4 and 5** to data from **bare margin, no spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, **piecewise linear** coefficient $d(t)$, and the resulting coefficients from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, with the same columns.

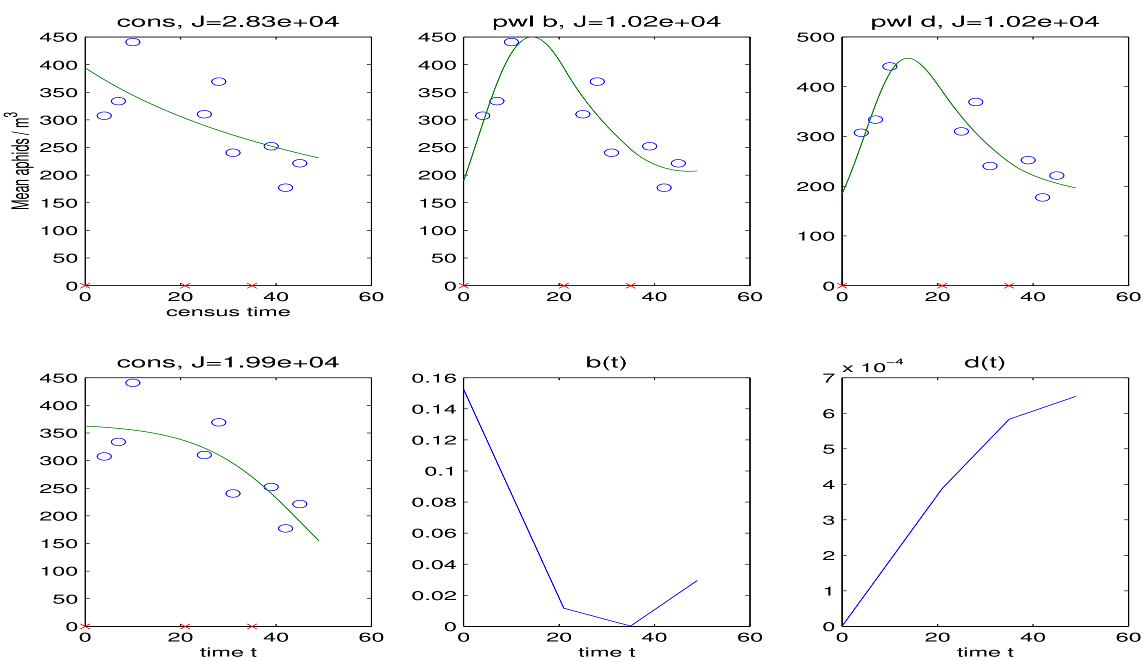

Figure 8: Fit of **logistic Model 6** to data from **bare margin, no spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, and **piecewise linear** coefficient $d(t)$ from left to right. Row 2 shows the resulting coefficients.

coeff type	var	Model 1 $\dot{N} = bN$	Model 2 $\dot{N} = -dN$	Model 3 $\dot{N} = aN\,(a \in \mathbb{R})$	Model 4 $\dot{N} = b - dN$	Model 5 $\dot{N} = bN - d$	Model 6 $\dot{N} = bN - dN^2$	Model 7 $\dot{N} = bN^2 - dN$
cons	J	5.2730e+04	2.6554e+04	2.6554e+04	2.6554e+04	2.0647e+04	2.8331e+04	1.9926e+04
pwc $b(t)$	J	5.2730e+04	n/a	1.5651e+04	1.1602e+04	1.6825e+04	1.1092e+04	1.7942e+04
	U	0.00		6.27	11.60	2.04	13.99	1.00
	$1-\alpha$	0.000		0.956	0.997	0.640	0.999	0.392
pwc $d(t)$	J	n/a	1.8592e+04	n/a	1.1621e+04	1.6343e+04	1.0974e+04	1.6093e+04
	U		3.85		11.56	2.37	14.23	2.14
	$1-\alpha$		0.854		0.997	0.694	0.999	0.658
cons	J	5.2730e+04	2.6554e+04	2.6554e+04	2.6554e+04	2.0647e+04	2.8333e+04	–
pwl $b(t)$	J	5.2730e+04	n/a	1.0123e+04	1.0514e+04	1.0054e+04	1.0193e+04	–
	U	0.00		14.61	13.73	9.48	16.02	
	$1-\alpha$	0.000		0.998	0.997	0.976	0.999	
pwl $d(t)$	J	n/a	1.8780e+04	n/a	1.0497e+04	1.0641e+04	1.0220e+04	–
	U		3.73		13.77	8.46	15.95	
	$1-\alpha$		0.707		0.997	0.963	0.999	

Table 3: Bare margin, no spray: Summary of cost function values and statistics.

Comments

- The exponential birth Model 1 fails to fit the data at all, regardless of incorporation of time-varying coefficients. Simple exponential death (Model 2) fits better, but we do not observe a statistically significant reduction in cost function when incorporating time-varying coefficients.
- Model 3 (exponential birth/death) performs very well when time-varying coefficients are used and their incorporation is statistically significant at the 95% confidence level (piecewise constant) and 99% confidence level (piecewise linear). Piecewise linear coefficients provide a much more eye-pleasing fit to the data.
- Of those remaining, Models 4, 5, and 6 with piecewise linear coefficients provide the best fit (smallest residual). In these cases, similar results are obtained for time-varying $b(t)$ and $d(t)$ and the addition of the time-varying coefficients proved statistically significant.
- Note that for Model 5, piecewise linear coefficients $d(t)$ substantially outperformed piecewise linear coefficients $b(t)$. In several other cases (though not all) $d(t)$ did better.
- In increasing order of least squares residual, the top models are: Model 3 (pwl) and Model 5 (pwl b); Model 6 (pwl b or d); Model 4 (pwl b or d); and Model 5 (pwl d). Some of the piecewise constant models are close behind.
- In general the smoother fit to data afforded by the piecewise linear coefficients seems better, an observation that carries across many of the datasets.

5.2 Dataset 2: Bare margin, low spray (15 g ai/ha)

coeff type	var	Model 1 $\dot{N} = bN$	Model 2 $\dot{N} = -dN$	Model 3 $\dot{N} = aN\ (a \in \mathbb{R})$	Model 4 $\dot{N} = b - dN$	Model 5 $\dot{N} = bN - d$	Model 6 $\dot{N} = bN - dN^2$	Model 7 $\dot{N} = bN^2 - dN$
cons	$b \mid a$	2.0250e-12	n/a	-3.0374e-03	6.0535e+01	1.3153e-01	4.7506e-01	7.6457e-07
	d	n/a	3.0374e-03	n/a	3.4554e-01	2.4256e+01	2.6964e-03	1.3749e-03
	N_0	168	181	181	0	184	44	171
	J	3.3972e+04	3.3400e+04	3.3400e+04	3.1845e+04	2.9606e+04	3.1578e+04	3.3665e+04
pwc	$b_1 \mid a_1$	3.8959e-03		1.3464e-02	4.7364e+01	6.8900e-02	4.1750e-01	1.0270e-04
$b(t)$	$b_2 \mid a_2$	4.7982e-12		5.7674e-03	4.2576e+01	5.4058e-02	3.0388e-01	1.0000e-08
or	$b_3 \mid a_3$	2.4463e-14		-6.9067e-02	2.2399e+01	4.1668e-10	1.7045e-01	1.0000e-08
$a(t)$	d	n/a	n/a	n/a	2.1076e-01	1.0137e+01	1.5364e-03	1.1592e-02
	N_0	157		149	0	159	22	171
	J	3.3788e+04		2.5052e+04	2.0878e+04	2.6216e+04	1.8391e+04	2.9559e+04
	U	0.05		3.00	4.73	1.16	6.45	1.25
	$1-\alpha$	0.024		0.777	0.906	0.441	0.960	0.465
pwc	b		n/a		4.5573e+01	1.6787e-02	3.8474e-01	6.0744e-05
$d(t)$	d_1		6.2478e-12		1.9468e-01	2.2374e-06	1.0826e-03	2.0720e-08
	d_2		1.5129e-13		2.2624e-01	4.2800e+00	1.9871e-03	3.6173e-03
	d_3	n/a	4.8032e-02	n/a	3.7782e-01	1.1132e+01	3.0940e-03	8.1449e-02
	N_0		185		0	146	19	154
	J		2.8057e+04		2.0410e+04	2.5669e+04	1.6874e+04	2.5269e+04
	U		1.71		5.04	1.38	7.84	2.99
	$1-\alpha$		0.576		0.920	0.498	0.980	0.776
cons	$b \mid a$	2.5252e-08	n/a	-3.0353e-03	6.0137e+01	1.8099e-01	4.6044e-01	
	d	n/a	3.0378e-03	n/a	3.4319e-01	3.3725e+01	2.6087e-03	–
	N_0	168	181	181	0	186	48	
	J	3.3972e+04	3.3400e+04	3.3400e+04	3.1845e+04	2.9342e+04	3.1560e+04	
pwl	$b_1 \mid a_1$	2.3707e-02		1.3174e-01	3.4034e+01	2.1311e-01	3.9487e-01	
$b(t)$	$b_2 \mid a_2$	1.1563e-09		-3.1967e-02	5.6314e+00	4.8078e-06	1.4407e-01	
or	$b_3 \mid a_3$	2.1590e-09		-1.5505e-02	3.5215e+00	4.0083e-02	1.2657e-01	
$a(t)$	$b_4 \mid a_4$	2.2143e-10		-8.0707e-02	1.4695e-02	2.4090e-02	5.7718e-07	
	d	n/a	n/a	n/a	4.6647e-02	9.9083e+00	7.9110e-04	–
	N_0	136		84	1	87	22	
	J	3.3096e+04		2.1561e+04	2.1264e+04	2.1675e+04	1.8950e+04	
	U	0.24		4.94	4.48	3.18	5.99	
	$1-\alpha$	0.029		0.824	0.786	0.636	0.888	
pwl	b		n/a		2.7680e+01	1.0840e-01	2.2110e-01	
$d(t)$	d_1		2.8235e-07		1.9038e-06	2.0837e-01	1.1753e-08	
	d_2		1.5570e-07		1.5439e-01	2.7443e+01	1.2122e-03	
	d_3		6.0576e-03		1.5257e-01	2.4820e+01	1.0543e-03	
	d_4	n/a	1.0895e-01	n/a	3.8542e-01	1.1829e+01	3.5480e-03	–
	N_0		183		5	98	44	
	J		2.9226e+04		2.0279e+04	2.2826e+04	1.7237e+04	
	U		1.29		5.13	2.57	7.48	
	$1-\alpha$		0.267		0.838	0.537	0.942	

Table 4: Bare margin, low spray: Optimal parameters and cost for constant versus piecewise constant coefficients for all models (top) and constant versus piecewise linear coefficients (bottom) for Models 1–6.

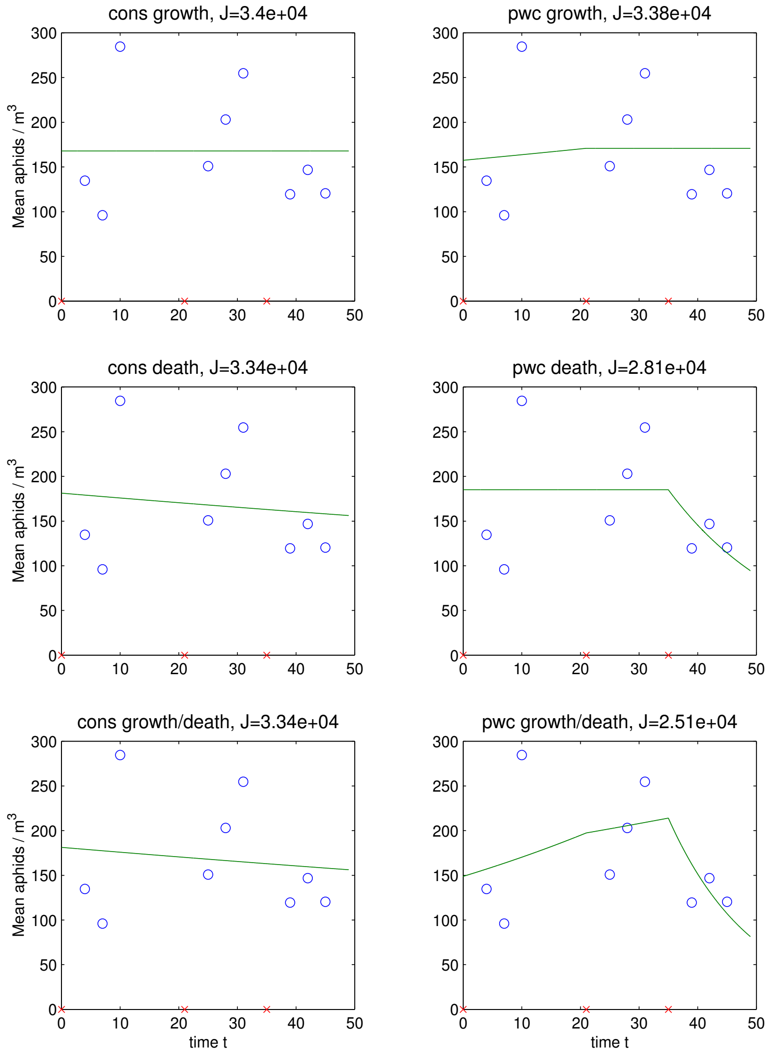

Figure 9: Fit of **exponential models** to data from **bare margin, low spray**. Coefficients are either constant (left column) or **piecewise constant** (right column). Rows 1–3 correspond to exponential models 1–3, respectively (birth, death, combined birth/death).

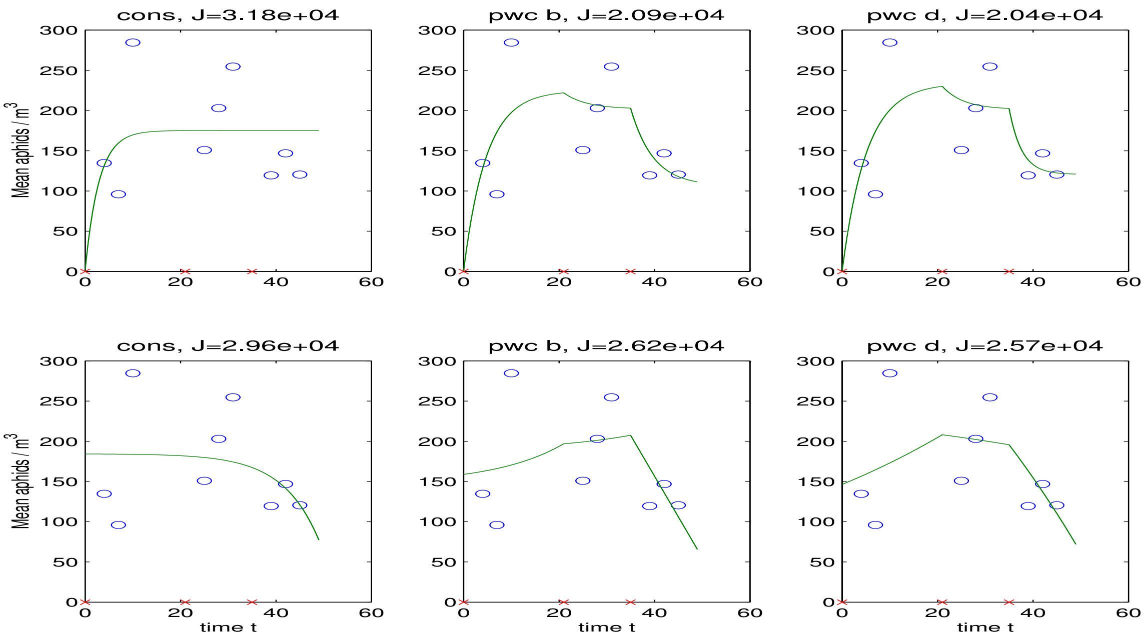

Figure 10: Fit of **Models 4 and 5** to data from **bare margin, low spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, again with results for constant and **piecewise constant** coefficients.

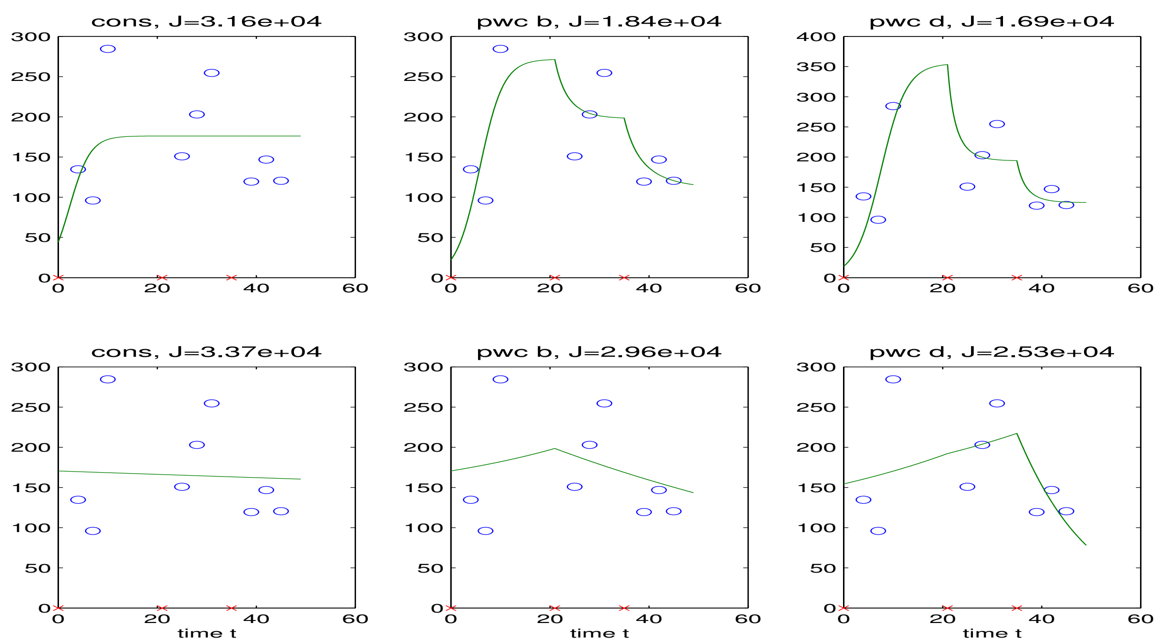

Figure 11: Fit of **logistic Models 6 and 7** to data from **bare margin, low spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN^2 - dN$, again with results for constant coefficients and **piecewise constant** coefficients.

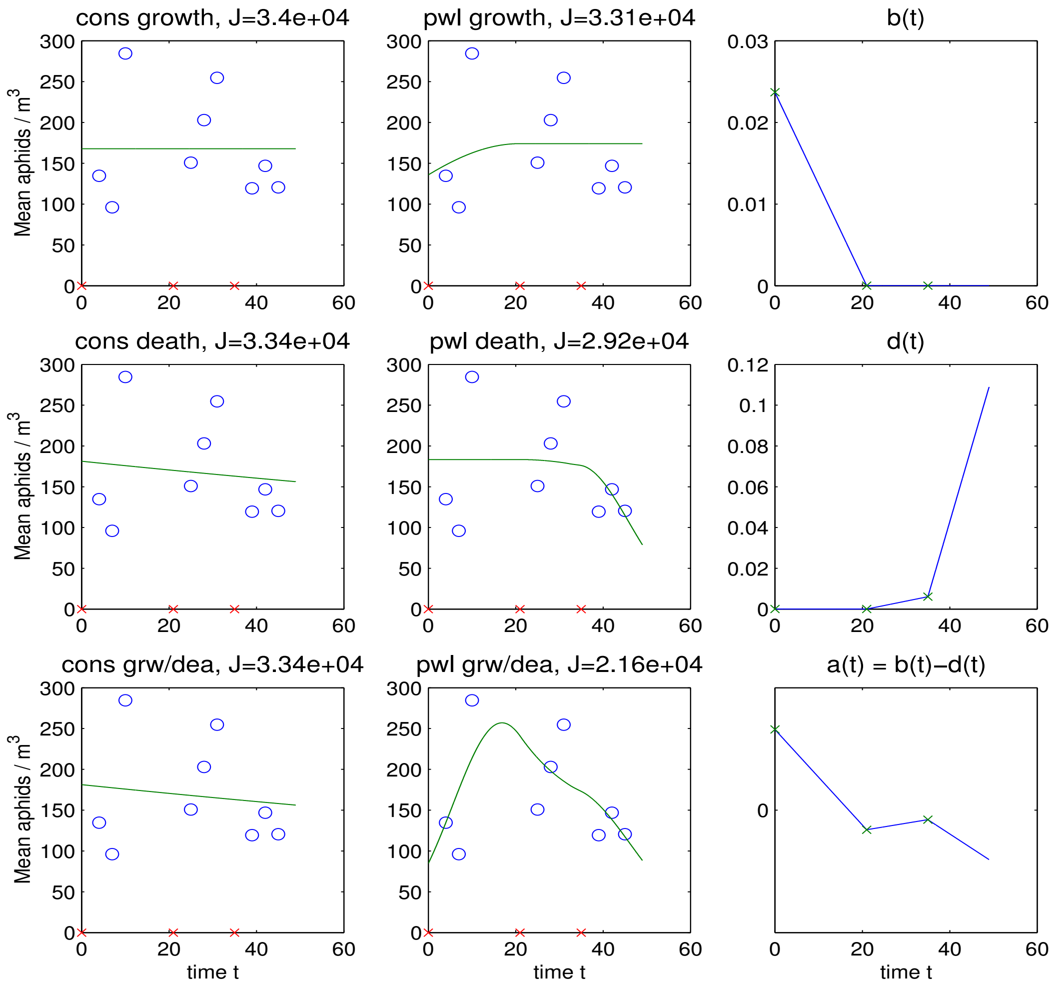

Figure 12: Fit of **exponential models** to data from **bare margin, low spray**. Coefficients are either constant (left column) or **piecewise linear** (center column) and pwl coefficients are shown in the right column. Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

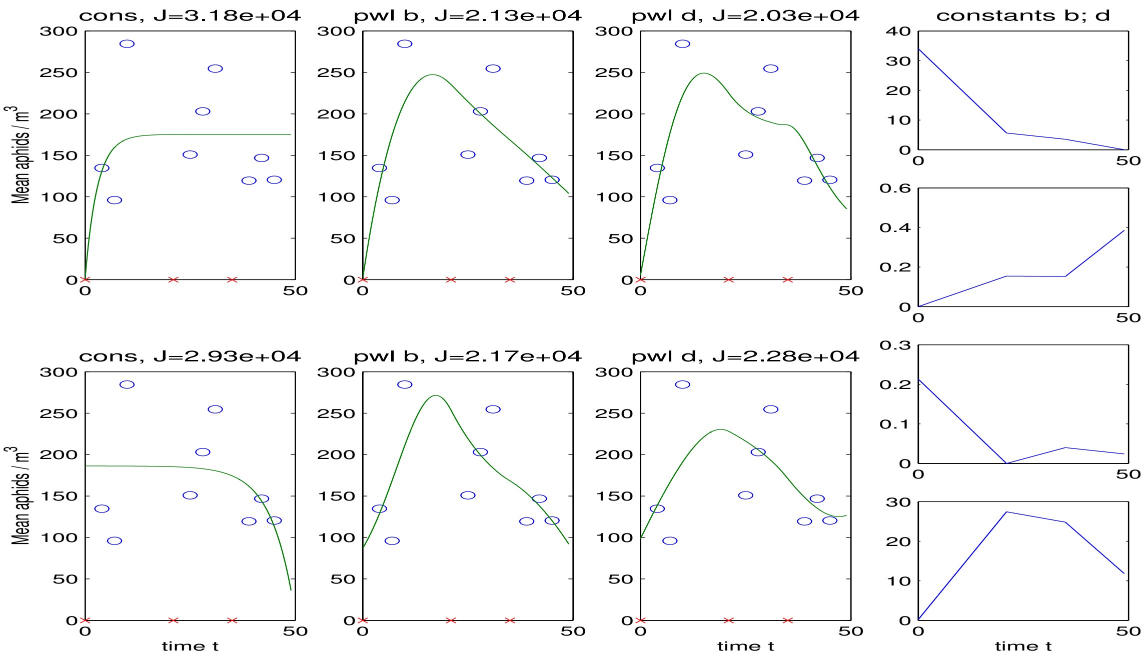

Figure 13: Fit of **Models 4 and 5** to data from **bare margin, low spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, **piecewise linear** coefficient $d(t)$, and the resulting coefficients from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, with the same columns.

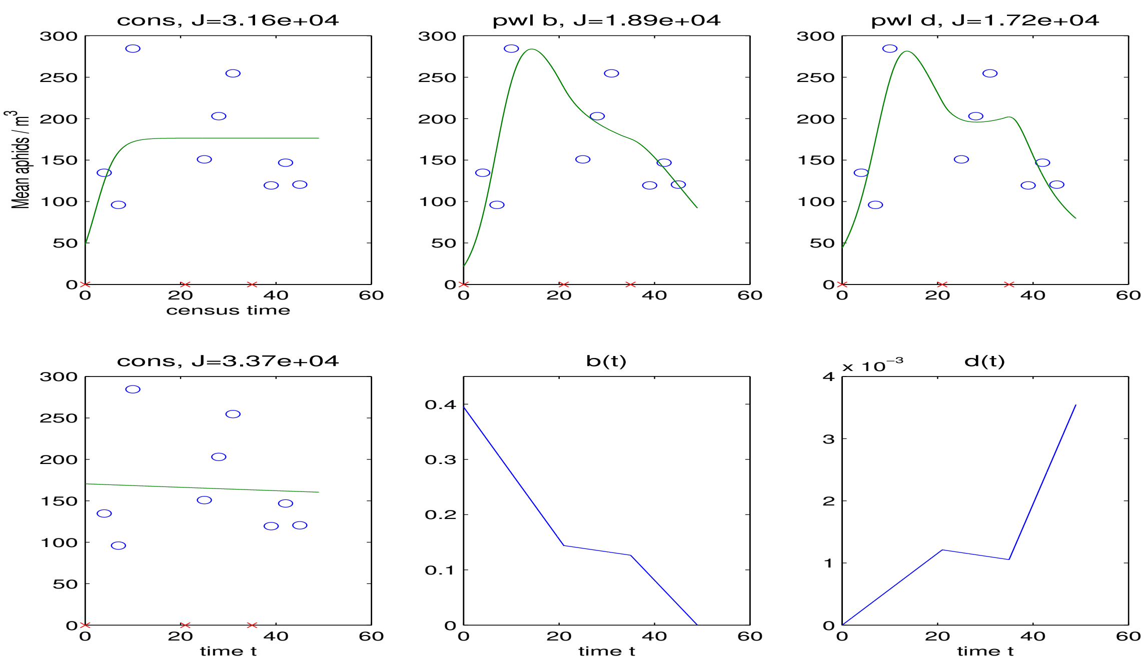

Figure 14: Fit of **logistic Model 6** to data from **bare margin, low spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, and **piecewise linear** coefficient $d(t)$ from left to right. Row 2 shows the resulting coefficients.

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	J	3.3972e+04	3.3400e+04	3.3400e+04	3.1845e+04	2.9606e+04	3.1578e+04	3.3665e+04
pwc $b(t)$	J	3.3788e+04		2.5052e+04	2.0878e+04	2.6216e+04	1.8391e+04	2.9559e+04
	U	0.05	n/a	3.00	4.73	1.16	6.45	1.25
	$1-\alpha$	0.024		0.777	0.906	0.441	0.960	0.465
pwc $d(t)$	J		2.8057e+04		2.0410e+04	2.5669e+04	1.6874e+04	2.5269e+04
	U	n/a	1.71	n/a	5.04	1.38	7.84	2.99
	$1-\alpha$		0.576		0.920	0.498	0.980	0.776
cons	J	3.3972e+04	3.3400e+04	3.3400e+04	3.1845e+04	2.9342e+04	3.1560e+04	–
pwl $b(t)$	J	3.3096e+04		2.1561e+04	2.1264e+04	2.1675e+04	1.8950e+04	
	U	0.24	n/a	4.94	4.48	3.18	5.99	–
	$1-\alpha$	0.029		0.824	0.786	0.636	0.888	
pwl $d(t)$	J		2.9226e+04		2.0279e+04	2.2826e+04	1.7237e+04	
	U	n/a	1.29	n/a	5.13	2.57	7.48	–
	$1-\alpha$		0.267		0.838	0.537	0.942	

Table 5: Bare margin, low spray: Summary of cost function values and statistics.

Comments

- Again, the exponential birth Model 1 fails to fit the data at all, either with constant or time-varying coefficients. For this dataset, exponential death performs a little better, but we still do not observe a statistically significant reduction in cost function when incorporating time-varying coefficients.
- Model 3 (exponential birth/death) performs decently with piecewise linear coefficients, though the reduction in cost is not statistically significant (p-value 0.824). Piecewise linear coefficients provide a much more eye-pleasing fit to data.
- To the eye, none of the models fit especially well, and we do not observe substantial improvement in moving to more complex models. In fact many of the models produce curves with similar characteristics.
- In increasing order of least squares residual, the top five models were: Model 6 (pwc d); Model 6 (pwl d); Model 6 (pwc b); Model 6 (pwl b); and Model 4 (pwc d, pwl d). For this dataset, time-varying coefficients $d(t)$ seem to be important, as do models with a stronger decay term.
- The logistic model (6) is the only model where significant reduction in cost function value occurs when adding time-varying coefficients. Here the piecewise constant and piecewise linear coefficients perform similarly. In this case, making the coefficient $d(t)$ time-varying makes a greater difference.

However, the penultimate conclusion is that the dataset itself seems an outlier when compared to model fits achieved with the other datasets.

5.3 Dataset 3: Bare margin, high spray (30 g ai/ha)

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	$b \mid a$	4.5924e-14	n/a	-9.8760e-03	8.2936e-07	1.1922e-01	2.0299e-09	3.6788e-06
	d	n/a	9.8758e-03	n/a	9.8779e-03	2.4558e+01	4.9736e-05	1.9885e-03
	N_0	169	216	216	216	205	212	161
	J	3.8614e+04	3.2146e+04	3.2146e+04	3.2146e+04	2.2070e+04	3.2994e+04	3.8633e+04
pwc	$b_1 \mid a_1$	2.4501e-14		2.2632e-02	1.0552e+02	3.4976e-01	1.6401e+00	1.3200e-04
$b(t)$	$b_2 \mid a_2$	2.4501e-14		-1.6214e-02	1.2550e+02	2.4203e-01	1.9446e+00	1.0000e-08
or	$b_3 \mid a_3$	2.4501e-14		-1.1007e-01	4.7118e+01	6.4372e-01	7.8234e-01	1.0000e-08
$a(t)$	d	n/a	n/a	n/a	5.4468e-01	6.3018e+01	8.5169e-03	1.3154e-02
	N_0	169		156	0	180	2	161
	J	3.8614e+04		1.3397e+04	9.2500e+03	1.1655e+04	9.3546e+03	2.7631e+04
	U	0.00		12.59	22.28	8.04	22.74	3.58
	$1-\alpha$	0.000		0.998	1.000	0.982	1.000	0.833
pwc	b		n/a		6.2436e+01	2.9248e-01	3.3735e-01	1.0085e-04
$d(t)$	d_1		3.9951e-13		2.9747e-01	5.6843e+01	1.5778e-03	5.7396e-06
	d_2		3.4107e-12		2.6465e-01	7.3294e+01	1.4458e-03	3.9238e-02
	d_3	n/a	1.1328e-01	n/a	7.0933e-01	2.2259e+01	4.0155e-03	1.2113e-01
	N_0		204		44	194	88	163
	J		1.6671e+04		8.2307e+03	1.1031e+04	8.4491e+03	1.3712e+04
	U		8.35		26.15	9.01	26.14	16.36
	$1-\alpha$		0.985		1.000	0.989	1.000	1.000
cons	$b \mid a$	8.8357e-11	n/a	-9.8693e-03	1.1533e-05	1.1743e-01	2.1707e-07	
	d	n/a	9.8756e-03	n/a	9.8862e-03	2.4186e+01	5.0075e-05	–
	N_0	169	216	216	216	205	212	
	J	3.8614e+04	3.2146e+04	3.2146e+04	3.2146e+04	2.2074e+04	3.2993e+04	
pwl	$b_1 \mid a_1$	4.4179e-12		2.4836e-02	2.4737e+01	1.0210e-01	1.4878e-01	
$b(t)$	$b_2 \mid a_2$	4.4191e-12		2.0486e-02	3.1409e+01	1.5955e-01	1.4464e-01	
or	$b_3 \mid a_3$	4.4208e-12		-1.0502e-01	3.5827e-03	1.5334e-02	7.9690e-07	
$a(t)$	$b_4 \mid a_4$	4.4182e-12		1.1666e-01	2.2753e+01	6.3370e-01	6.0767e-02	
	d	n/a	n/a	n/a	1.0910e-01	2.4353e+01	5.2798e-04	–
	N_0	169		154	122	204	114	
	J	3.8614e+04		1.1290e+04	1.0724e+04	9.5268e+03	1.2420e+04	
	U	0.00		16.62	17.98	11.85	14.91	
	$1-\alpha$	0.000		0.999	1.000	0.992	0.998	
pwl	b		n/a		4.6702e+00	1.2392e-01	4.4446e+00	
$d(t)$	d_1		3.1732e-08		3.1028e-07	1.4250e+01	2.6468e-02	
	d_2		2.9956e-14		2.5643e-05	2.7196e+01	1.9865e-02	
	d_3		5.1669e-02		1.2357e-01	3.5305e+01	1.8867e-02	
	d_4	n/a	2.9376e-02	n/a	2.4074e-06	2.8641e-07	8.9076e-02	–
	N_0		210		149	153	702	
	J		1.9002e+04		1.1774e+04	1.0619e+04	1.1604e+04	
	U		6.23		15.57	9.71	16.59	
	$1-\alpha$		0.899		0.999	0.979	0.999	

Table 6: Bare margin, high spray: Optimal parameters and cost for constant versus piecewise constant coefficients for all models (top) and constant versus piecewise linear coefficients (bottom) for Models 1–6.

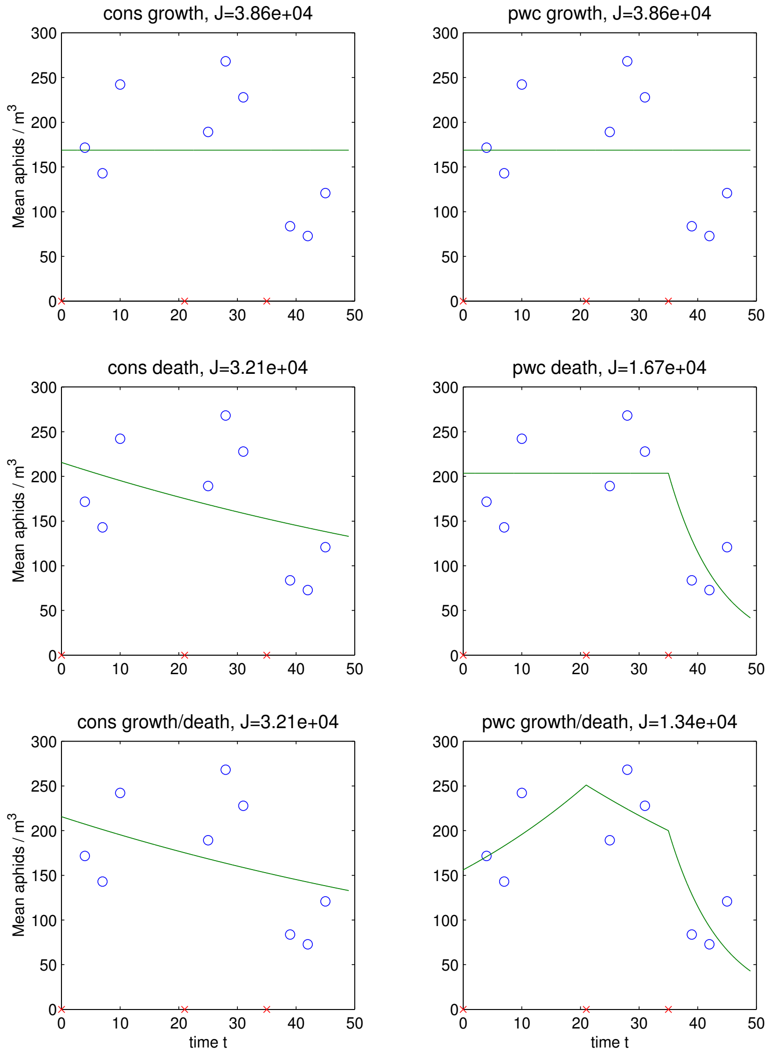

Figure 15: Fit of **exponential models** to data from **bare margin, high spray**. Coefficients are either constant (left column) or **piecewise constant** (right column). Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

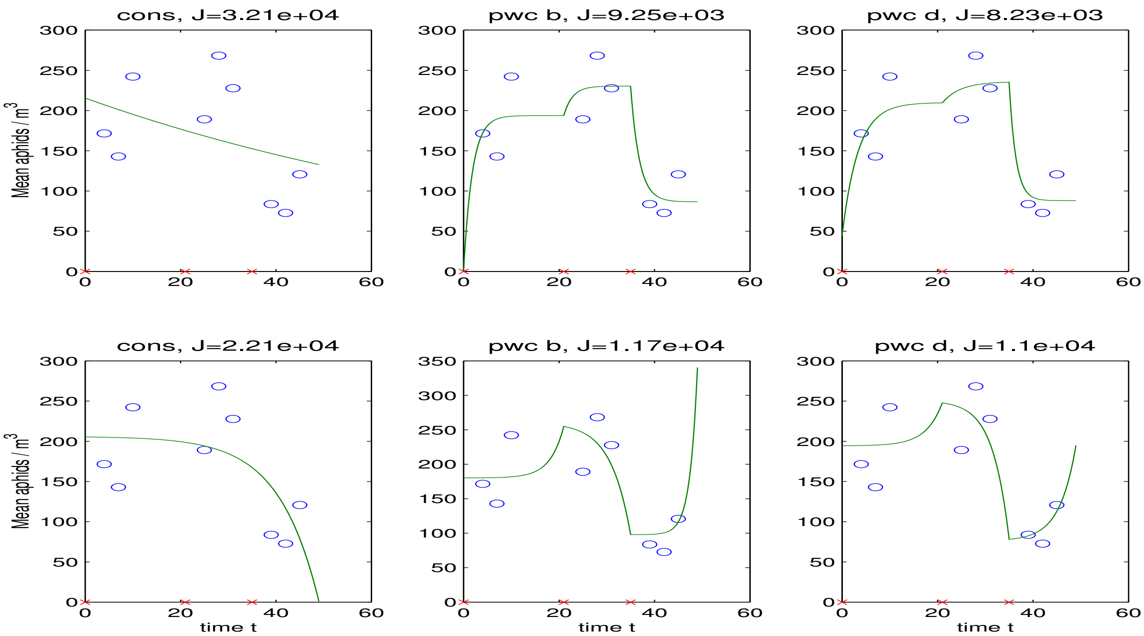

Figure 16: Fit of **Models 4 and 5** to data from **bare margin, high spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, again with results for constant and **piecewise constant** coefficients.

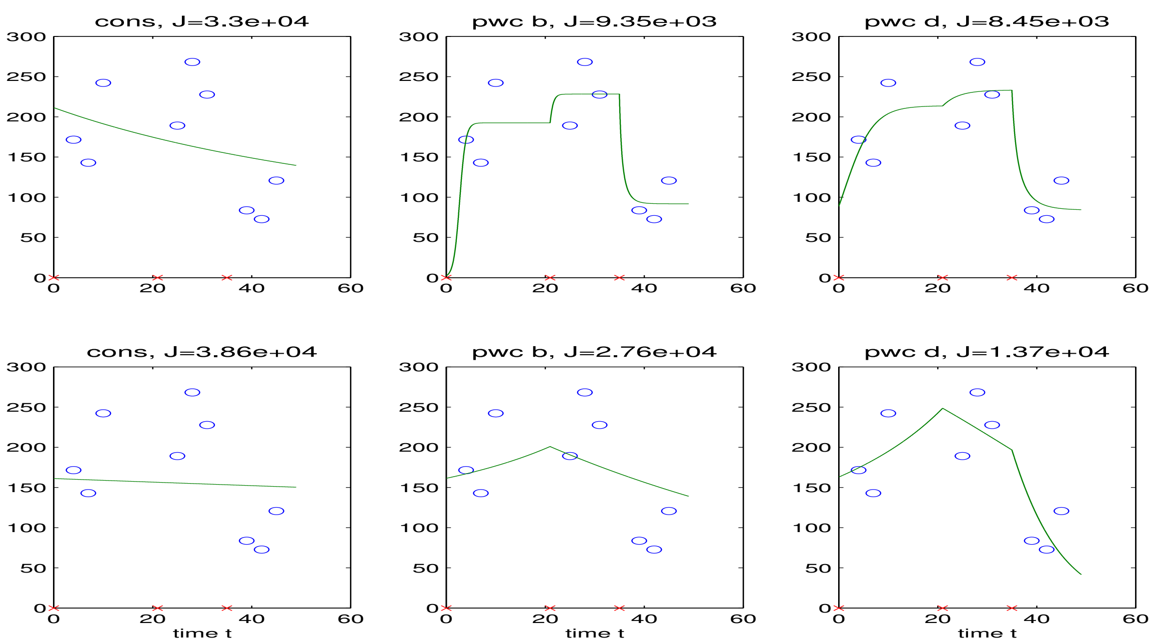

Figure 17: Fit of **logistic Models 6 and 7** to data from **bare margin, high spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN^2 - dN$, again with results for constant coefficients and **piecewise constant** coefficients.

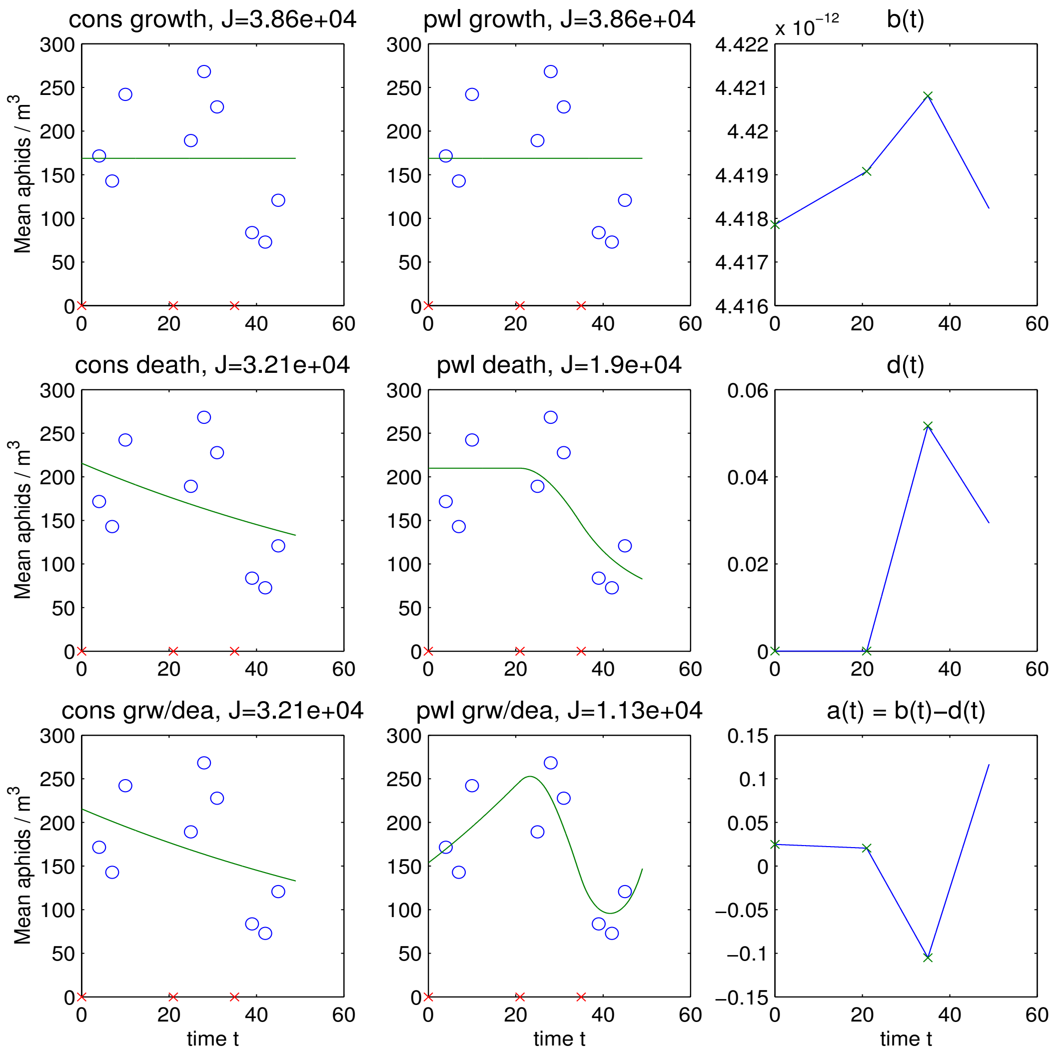

Figure 18: Fit of **exponential models** to data from **bare margin, high spray**. Coefficients are either constant (left column) or **piecewise linear** (center column) and pwl coefficients are shown in the right column. Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

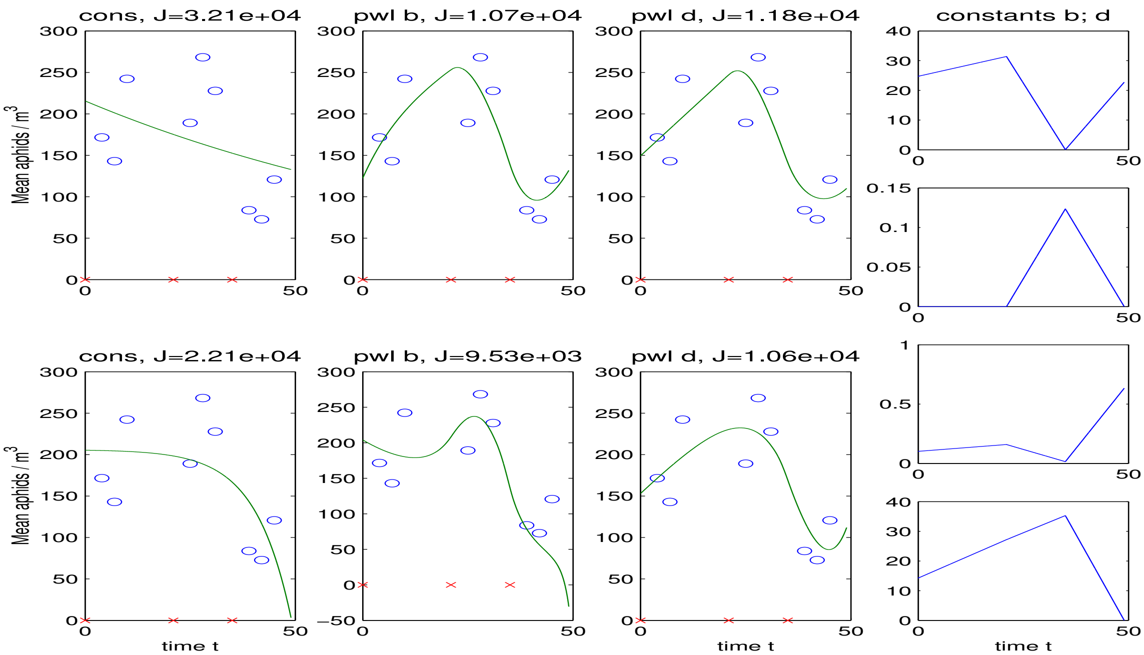

Figure 19: Fit of **Models 4 and 5** to data from **bare margin, high spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, **piecewise linear** coefficient $d(t)$, and the resulting coefficients from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, with the same columns.

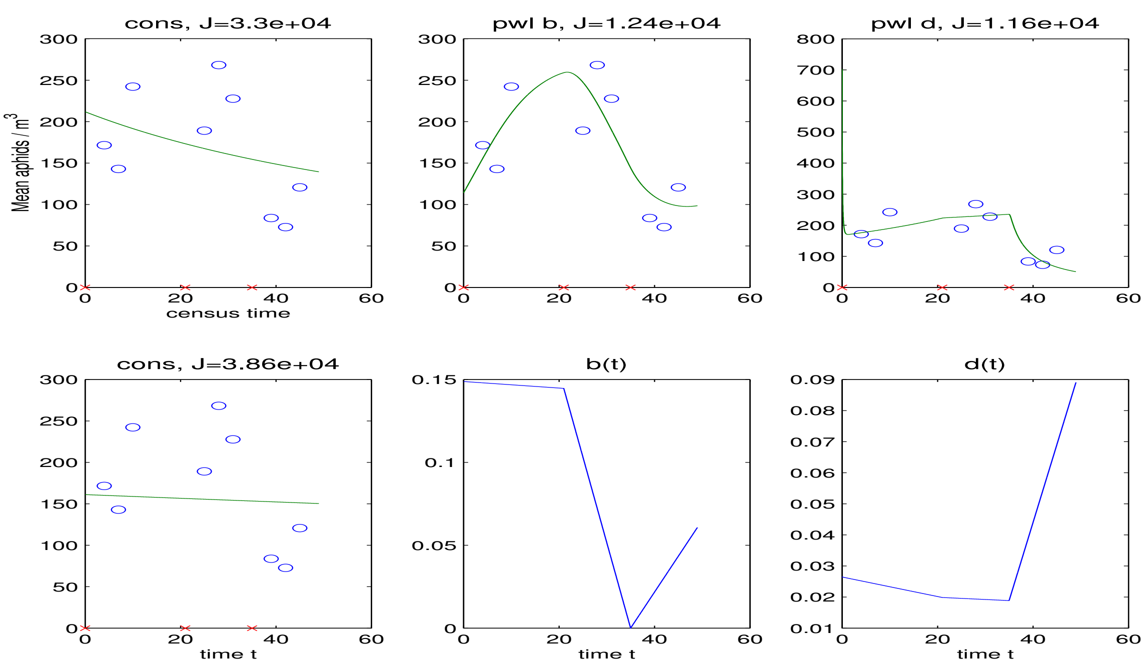

Figure 20: Fit of **logistic Model 6** to data from **bare margin, high spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, and **piecewise linear** coefficient $d(t)$ from left to right. Row 2 shows the resulting coefficients.

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN \, (a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	J	3.8614e+04	3.2146e+04	3.2146e+04	3.2146e+04	2.2070e+04	3.2994e+04	3.8633e+04
pwc $b(t)$	J	3.8614e+04	n/a	1.3397e+04	9.2500e+03	1.1655e+04	9.3546e+03	2.7631e+04
	U	0.00		12.59	22.28	8.04	22.74	3.58
	$1-\alpha$	0.000		0.998	1.000	0.982	1.000	0.833
pwc $d(t)$	J	n/a	1.6671e+04	n/a	8.2307e+03	1.1031e+04	8.4491e+03	1.3712e+04
	U		8.35		26.15	9.01	26.14	16.36
	$1-\alpha$		0.985		1.000	0.989	1.000	1.000
cons	J	3.8614e+04	3.2146e+04	3.2146e+04	3.2146e+04	2.2074e+04	3.2993e+04	–
pwl $b(t)$	J	3.8614e+04	n/a	1.1290e+04	1.0724e+04	9.5268e+03	1.2420e+04	–
	U	0.00		16.62	17.98	11.85	14.91	
	$1-\alpha$	0.000		0.999	1.000	0.992	0.998	
pwl $d(t)$	J	n/a	1.9002e+04	n/a	1.1774e+04	1.0619e+04	1.1604e+04	–
	U		6.23		15.57	9.71	16.59	
	$1-\alpha$		0.899		0.999	0.979	0.999	

Table 7: Bare margin, high spray: Summary of cost function values and statistics.

Comments

- Again, the exponential birth model fails to fit the data at all, regardless of incorporation of time-varying coefficients. The exponential birth model does better, and we observe a statistically significant reduction in cost function value when incorporating piecewise constant coefficients (p-value 0.985), but not piecewise linear (p-value 0.899).

- Model 3 (exponential birth/death) performs very well when time-varying coefficients are used and their incorporation is statistically significant at the 99% confidence level (for both types). Piecewise linear coefficients provide a much more eye-pleasing fit to data—the trajectories based on piecewise constant coefficients are probably not realistic—they are not smooth enough.

- Of the remaining models, Models 4 and 6 for piecewise constant coefficients and Model 5 for piecewise linear coefficients leave the smallest least squares residuals. For Models 4, 5, and 6 we see statistically significant cost function reduction with all types of time-varying coefficients.

- In increasing order of least squares residual, the top models are: Model 4 (pwc d); Model 6 (pwc d); Model 4 (pwc b); Model 6 (pwc b); Model 5 (pwl b). Models 4 and 5 with piecewise linear coefficients did decently as well. Again, despite the improved residual performance of piecewise constant coefficients, the resulting trajectories are less than satisfactory.

- Note that for the top models, piecewise constant coefficients $d(t)$ always slightly outperformed (lower residuals) piecewise constant $b(t)$. In two of three piecewise linear cases, $b(t)$ did better. Hence in these models, there is no clear preference for nonconstant d versus nonconstant b.

5.4 Dataset 4: Weedy margin, no spray

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	$b \mid a$	9.8004e-12	n/a	-2.1543e-02	8.1953e-08	6.5262e-02	1.6842e-09	5.4344e-04
	d	n/a	2.1543e-02	n/a	2.1540e-02	2.6198e+01	7.0315e-05	1.5995e-01
	N_0	265	442	442	442	384	453	294
	J	1.2048e+05	4.5489e+04	4.5489e+04	4.5489e+04	2.1328e+04	5.3614e+04	4.3110e+04
pwc	$b_1 \mid a_1$	2.5147e-14		2.3544e-02	3.7966e+01	7.2213e-02	1.4225e-01	5.5449e-04
$b(t)$	$b_2 \mid a_2$	2.3373e-14		-7.5684e-02	5.8976e-06	2.7080e-08	1.4619e-02	2.7780e-04
or	$b_3 \mid a_3$	2.3380e-14		-5.2870e-02	1.2700e+00	1.3430e-01	1.0000e-09	9.1028e-04
$a(t)$	d	n/a	n/a	n/a	6.8451e-02	2.2408e+01	2.6676e-04	1.6105e-01
	N_0	265		311	259	344	252	294
	J	1.2048e+05		1.1893e+04	1.1568e+04	1.2602e+04	1.4430e+04	2.7067e+04
	U	0.00		25.42	26.39	6.23	24.44	5.33
	$1-\alpha$	0.000		1.000	1.000	0.956	1.000	0.931
pwc	b		n/a		1.5291e+01	1.5299e-02	6.7662e-02	4.9393e-05
$d(t)$	d_1		4.2229e-14		9.1163e-03	2.3272e-06	8.0262e-05	4.1299e-08
	d_2		3.6283e-02		1.2106e-01	2.6406e+01	4.1097e-04	8.9448e-02
	d_3	n/a	8.8726e-02	n/a	1.7576e-01	6.1436e+00	1.0111e-03	5.8343e-02
	N_0		377		282	329	278	326
	J		1.7264e+04		1.1679e+04	1.2153e+04	1.1599e+04	1.2231e+04
	U		14.71		26.05	6.79	32.60	22.72
	$1-\alpha$		0.999		1.000	0.967	1.000	1.000
cons	$b \mid a$	4.2141e-13	n/a	-2.1539e-02	1.6693e-05	6.5242e-02	1.7204e-07	
	d	n/a	2.1539e-02	n/a	2.1548e-02	2.6190e+01	6.9588e-05	–
	N_0	265	442	442	442	384	449	
	J	1.2048e+05	4.5489e+04	4.5489e+04	4.5489e+04	2.1328e+04	5.3610e+04	
pwl	$b_1 \mid a_1$	4.3299e-14		7.8328e-02	5.7083e+01	1.5860e-01	3.5225e+00	
$b(t)$	$b_2 \mid a_2$	4.3275e-14		-2.7575e-02	3.0603e+01	1.3154e-02	5.0008e+00	
or	$b_3 \mid a_3$	4.3276e-14		-8.8266e-02	9.7539e-05	3.0423e-02	1.6283e+00	
$a(t)$	$b_4 \mid a_4$	4.3301e-14		8.2007e-03	1.2757e+01	2.5953e-01	9.3088e-01	
	d	n/a	n/a	n/a	9.6290e-02	2.2834e+01	1.0922e-02	–
	N_0	265		243	217	245	356	
	J	1.2048e+05		1.1162e+04	1.2553e+04	1.1043e+04	1.2029e+04	
	U	0.00		27.68	23.61	8.38	31.11	
	$1-\alpha$	0.000		1.000	1.000	0.961	1.000	
pwl	b		n/a		2.0854e+01	1.1896e-01	6.4854e-02	
$d(t)$	d_1		8.6766e-10		2.6427e-07	1.0260e+01	1.4981e-08	
	d_2		1.1205e-08		6.5134e-02	6.7053e+01	1.8816e-04	
	d_3		9.5705e-02		1.9913e-01	3.7494e+01	6.9877e-04	
	d_4	n/a	6.1553e-08	n/a	2.2829e-01	4.4823e+00	1.2667e-03	–
	N_0		369		252	250	253	
	J		1.4967e+04		1.1372e+04	1.1308e+04	1.1223e+04	
	U		18.35		27.00	7.97	33.99	
	$1-\alpha$		1.000		1.000	0.953	1.000	

Table 8: Weedy margin, no spray: Optimal parameters and cost for constant versus piecewise constant coefficients for all models (top) and constant versus piecewise linear coefficients (bottom) for Models 1–6.

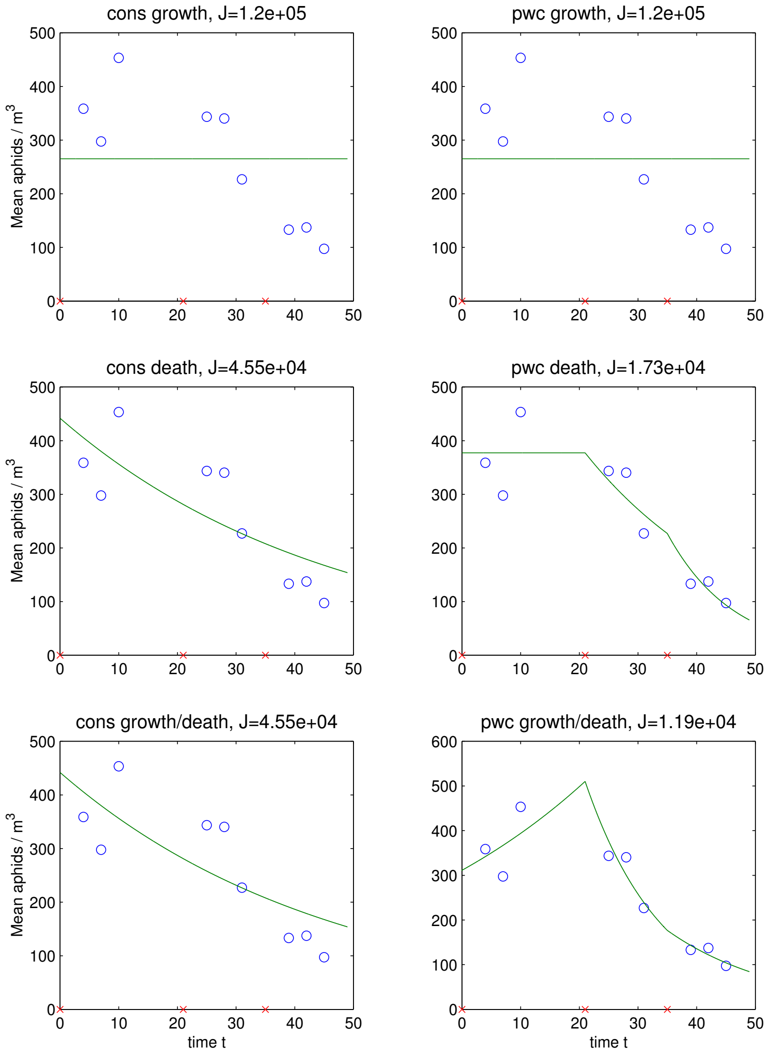

Figure 21: Fit of **exponential models** to data from **weedy margin, no spray**. Coefficients are either constant (left column) or **piecewise constant** (right column). Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

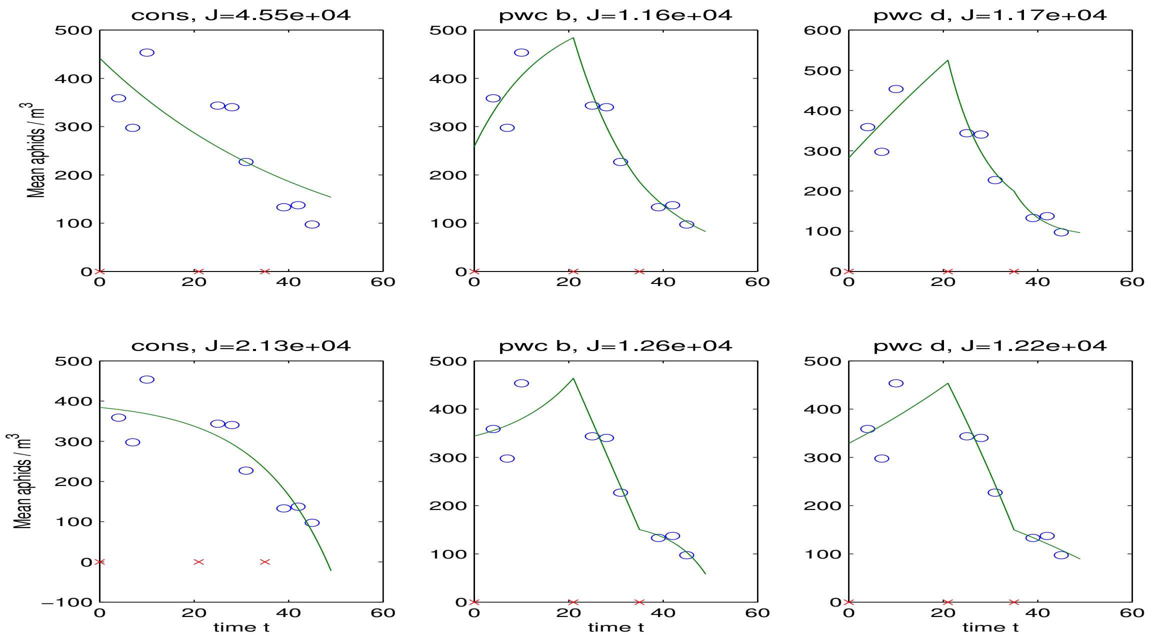

Figure 22: Fit of **Models 4 and 5** to data from **weedy margin, no spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, again with results for constant and **piecewise constant** coefficients.

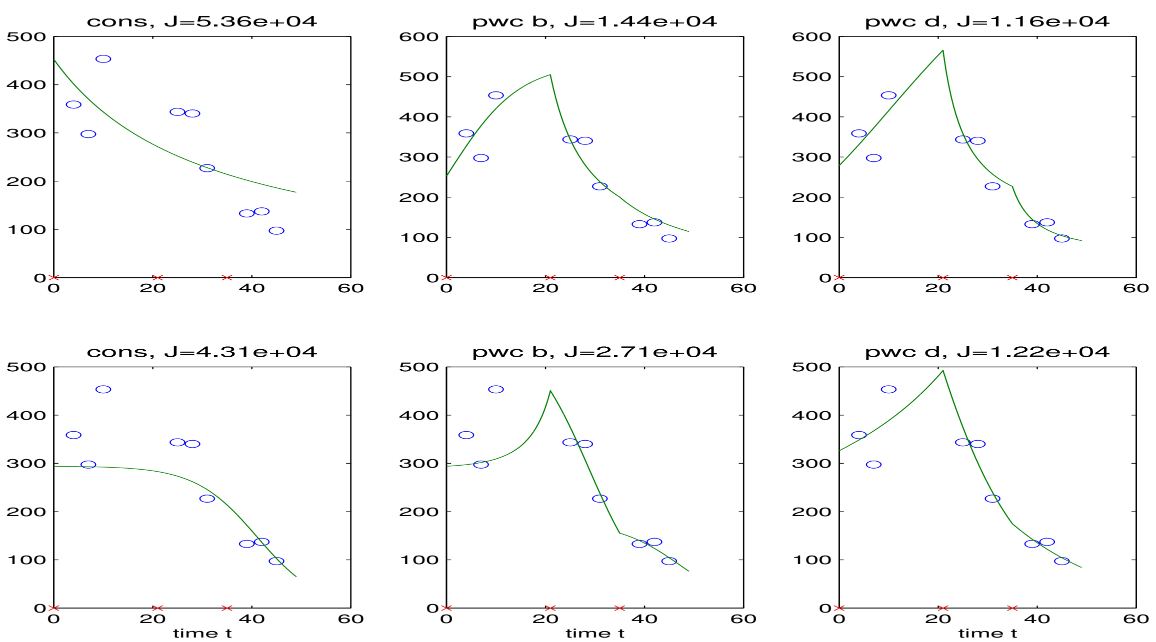

Figure 23: Fit of **logistic Models 6 and 7** to data from **weedy margin, no spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN^2 - dN$, again with results for constant coefficients and **piecewise constant** coefficients.

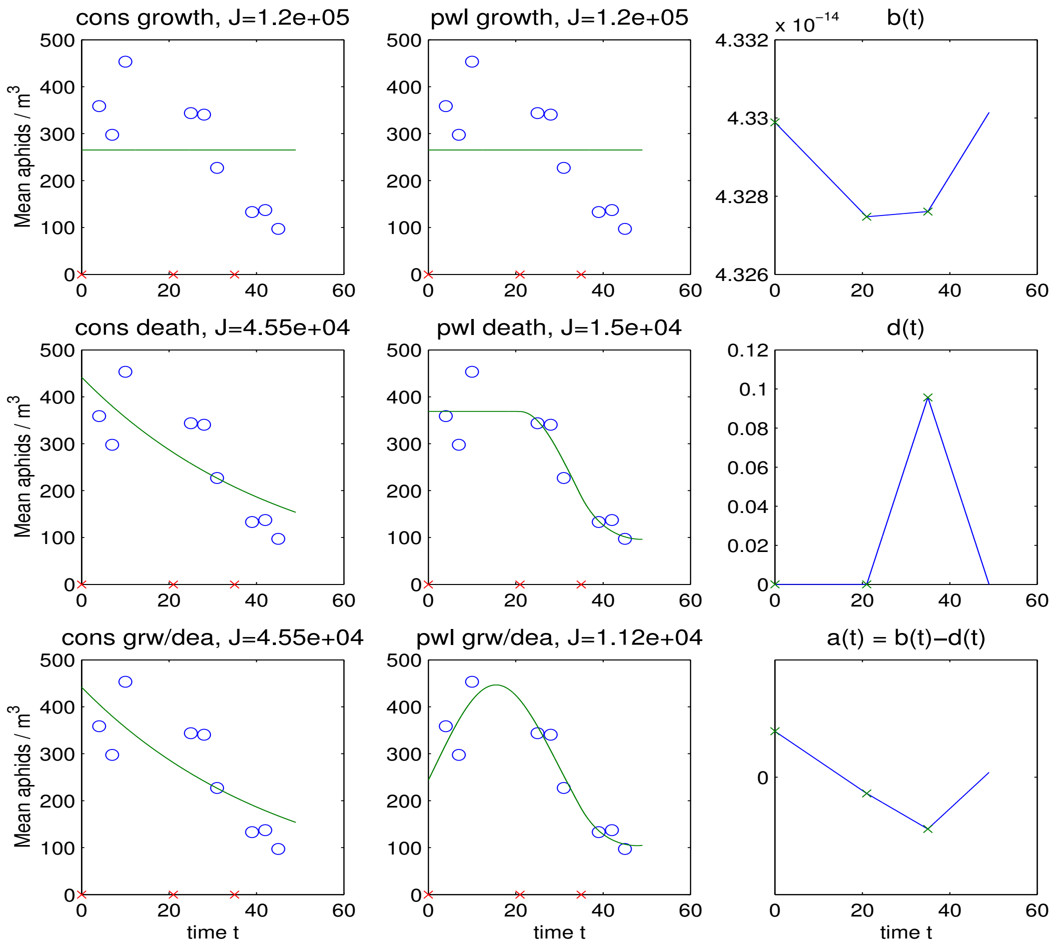

Figure 24: Fit of **exponential models** to data from **weedy margin, no spray**. Coefficients are either constant (left column) or **piecewise linear** (center column) and pwl coefficients are shown in the right column. Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

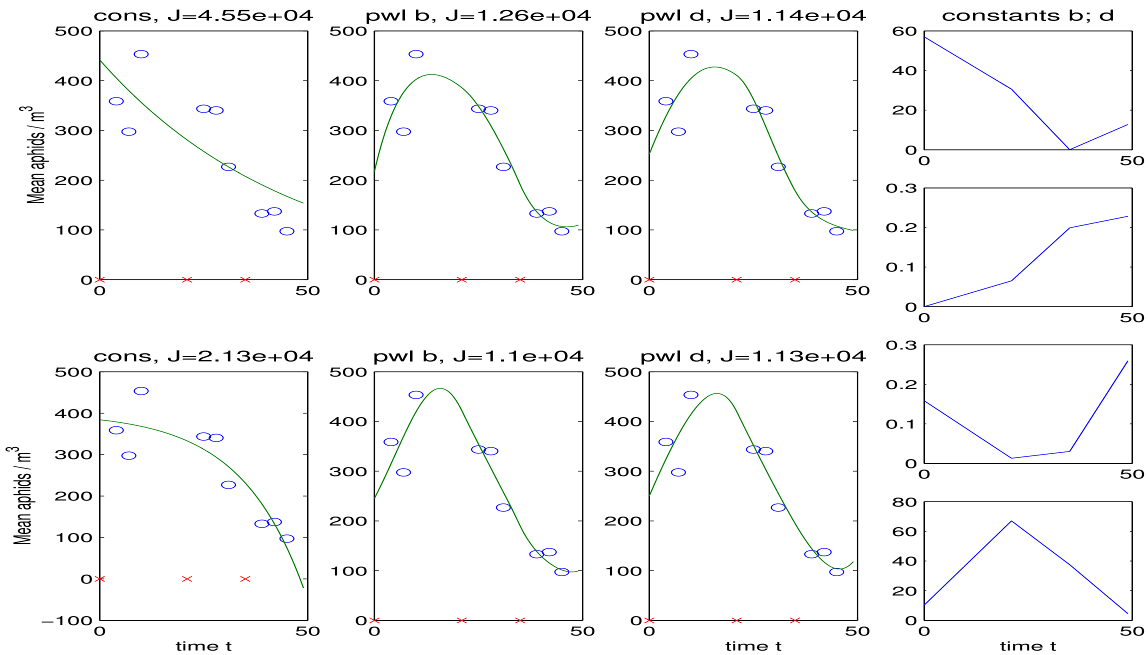

Figure 25: Fit of **Models 4 and 5** to data from **weedy margin, no spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, **piecewise linear** coefficient $d(t)$, and the resulting coefficients from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, with the same columns.

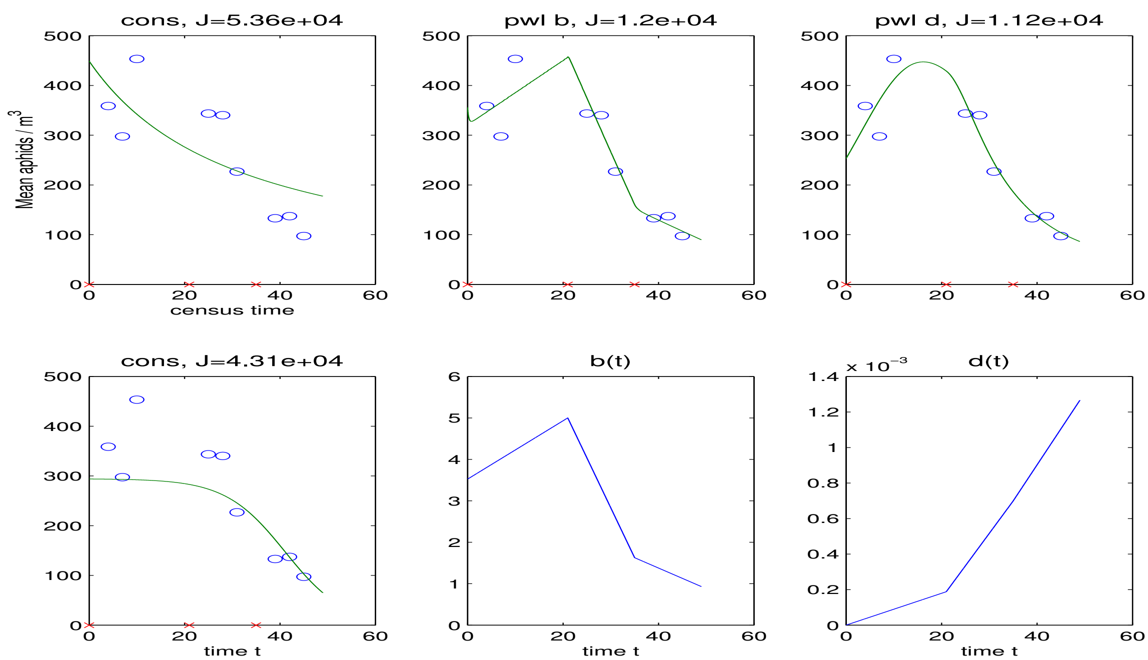

Figure 26: Fit of **logistic Model 6** to data from **weedy margin, no spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, and **piecewise linear** coefficient $d(t)$ from left to right. Row 2 shows the resulting coefficients.

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN \; (a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	J	1.2048e+05	4.5489e+04	4.5489e+04	4.5489e+04	2.1328e+04	5.3614e+04	4.3110e+04
pwc $b(t)$	J	1.2048e+05		1.1893e+04	1.1568e+04	1.2602e+04	1.4430e+04	2.7067e+04
	U	0.00	n/a	25.42	26.39	6.23	24.44	5.33
	$1-\alpha$	0.000		1.000	1.000	0.956	1.000	0.931
pwc $d(t)$	J		1.7264e+04		1.1679e+04	1.2153e+04	1.1599e+04	1.2231e+04
	U	n/a	14.71	n/a	26.05	6.79	32.60	22.72
	$1-\alpha$		0.999		1.000	0.967	1.000	1.000
cons	J	1.2048e+05	4.5489e+04	4.5489e+04	4.5489e+04	2.1328e+04	5.3610e+04	–
pwl $b(t)$	J	1.2048e+05		1.1162e+04	1.2553e+04	1.1043e+04	1.2029e+04	
	U	0.00	n/a	27.68	23.61	8.38	31.11	–
	$1-\alpha$	0.000		1.000	1.000	0.961	1.000	
pwl $d(t)$	J		1.4967e+04		1.1372e+04	1.1308e+04	1.1223e+04	
	U	n/a	18.35	n/a	27.00	7.97	33.99	–
	$1-\alpha$		1.000		1.000	0.953	1.000	

Table 9: Weedy margin, no spray: Summary of cost function values and statistics.

Comments

- The exponential birth model fails to fit the data at all, regardless of incorporation of time-varying coefficients. The exponential death model performs better, and we again observe a statistically significant reduction in cost function when incorporating time-varying coefficients of either type.
- For constant coefficients, Model 3 (exponential birth/death) leaves the same least squares residual as Model 2, but Model 3 performs very well when time-varying coefficients are used. The incorporation of either type of time-varying coefficients is statistically significant at the 99% confidence level. Both piecewise constant and piecewise linear coefficients yield an eye-pleasing fit to the data.
- For Models 4 through 7, piecewise coefficients $d(t)$ often outperformed time-varying $b(t)$ (5 out of 7 fits).
- For Models 4 through 6, we observe statistically significant improvement when adding any kind of time-varying coefficients.
- In increasing order of least squares residual, the top models were: Model 5 (pwl b); Model 3 (pwl) and Model 6 (pwl d); Model 5 (pwl d); and Model 4 (pwl d). Models 3 and 4 also performed well with piecewise constant coefficients. Note that the best of these models (the first few) give a rather satisfactory curve when compared to data as well as providing a small residual.

5.5 Dataset 5: Weedy margin, low spray (15 g ai/ha)

coeff type	var	Model 1 $\dot{N} = bN$	Model 2 $\dot{N} = -dN$	Model 3 $\dot{N} = aN\,(a \in \mathbb{R})$	Model 4 $\dot{N} = b - dN$	Model 5 $\dot{N} = bN - d$	Model 6 $\dot{N} = bN - dN^2$	Model 7 $\dot{N} = bN^2 - dN$
cons	$b \mid a$	6.6751e-11	n/a	-5.8838e-02	2.7200e-07	1.5115e-08	3.4690e-09	5.9792e-05
	d	n/a	5.8838e-02	n/a	5.8838e-02	6.7174e+00	3.4779e-04	6.8318e-02
	N_0	124	391	391	391	296	545	369
	J	9.5130e+04	1.8532e+03	1.8532e+03	1.8532e+03	8.7019e+03	6.7551e+03	1.7755e+03
pwc $b(t)$ or $a(t)$	$b_1 \mid a_1$	1.5142e-13	n/a	-5.5741e-02	5.9520e+01	5.6285e-02	3.2032e-01	2.4750e-04
	$b_2 \mid a_2$	2.3412e-14		-6.8120e-02	2.7251e-01	3.0800e-01	1.9913e-08	1.2574e-03
	$b_3 \mid a_3$	2.3379e-14		-4.4933e-02	8.2282e-01	6.3783e-01	1.7516e-02	9.2546e-04
	d	n/a		n/a	1.8618e+00	2.3649e+01	1.3902e-03	1.2185e-01
	N_0	124		384	469	315	1199	360
	J	9.5130e+04		1.8312e+03	7.4849e+02	1.3656e+03	2.2279e+03	1.5789e+03
	U	0.00		0.11	13.28	48.35	18.29	1.12
	$1-\alpha$	0.000		0.053	0.999	1.000	1.000	0.429
pwc $d(t)$	b	n/a	n/a	n/a	5.9535e+01	7.8239e-03	3.0849e-01	4.0406e-04
	d_1		5.5753e-02		2.7257e-01	1.3973e+01	1.3409e-03	1.5350e-01
	d_2		6.8083e-02		8.2301e-01	3.0839e+00	4.7083e-03	4.7980e-02
	d_3		4.4992e-02		1.8623e+00	2.8437e+00	1.0584e-02	1.1272e-01
	N_0		384		469	346	1200	332
	J		1.8312e+03		7.4849e+02	1.4425e+03	9.7652e+02	1.3795e+03
	U		0.11		13.28	45.29	53.26	2.58
	$1-\alpha$		0.053		0.999	1.000	1.000	0.725
cons	$b \mid a$	1.8330e-09	n/a	-5.8838e-02	2.3021e-04	2.1963e-08	1.8188e-08	–
	d	n/a	5.8838e-02	n/a	5.8844e-02	6.7206e+00	3.6553e-04	
	N_0	124	391	391	391	296	594	
	J	9.5130e+04	1.8532e+03	1.8532e+03	1.8532e+03	8.7019e+03	6.4203e+03	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	9.2193e-11	n/a	-3.3683e-02	2.8752e+02	8.4129e-03	2.8839e+00	–
	$b_2 \mid a_2$	9.1650e-11		-7.3455e-02	7.8893e+01	2.4245e-07	7.4802e-01	
	$b_3 \mid a_3$	9.2025e-11		-5.3253e-02	4.0544e+01	1.3981e-01	3.5859e-01	
	$b_4 \mid a_4$	9.2392e-11		-6.0475e-03	1.7750e+01	5.1982e-01	1.3565e-01	
	d	n/a		n/a	8.7911e-01	1.0265e+01	8.3909e-03	
	N_0	124		350	624	318	561	
	J	9.5130e+04		1.5607e+03	1.4132e+03	1.7449e+03	1.4158e+03	
	U	0.00		1.69	2.80	35.88	31.81	
	$1-\alpha$	0.000		0.360	0.577	1.000	1.000	
pwl $d(t)$	b	n/a	n/a	n/a	2.0126e+01	1.0683e-01	8.0585e-02	–
	d_1		3.3225e-02		4.7440e-02	5.3526e+01	3.6872e-05	
	d_2		7.3681e-02		2.7414e-01	1.7864e+01	1.3836e-03	
	d_3		5.3216e-02		3.4298e-01	7.7182e+00	2.1305e-03	
	d_4		3.7473e-03		1.1723e+00	9.7573e-09	7.1794e-03	
	N_0		349		302	362	259	
	J		1.5603e+03		1.4831e+03	1.6453e+03	1.6980e+03	
	U		1.69		2.25	38.60	25.03	
	$1-\alpha$		0.361		0.477	1.000	1.000	

Table 10: Weedy margin, low spray: Optimal parameters and cost for constant versus piecewise constant coefficients for all models (top) and constant versus piecewise linear coefficients (bottom) for Models 1–6.

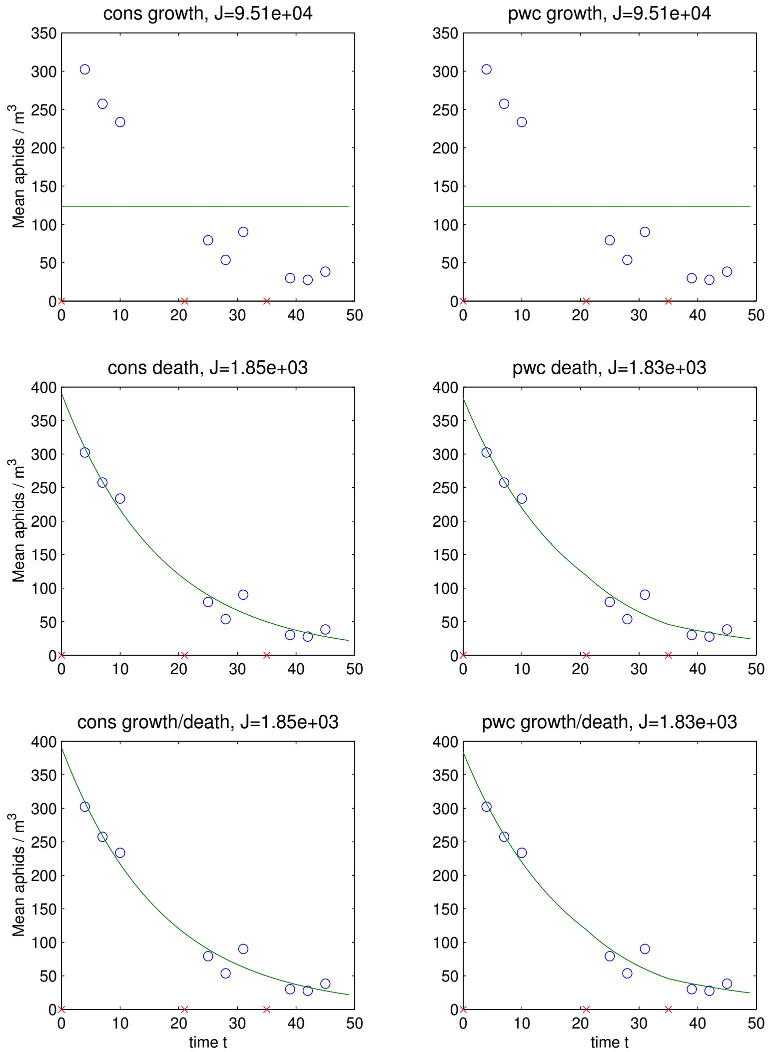

Figure 27: Fit of **exponential models** to data from **weedy margin, low spray**. Coefficients are either constant (left column) or **piecewise constant** (right column). Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

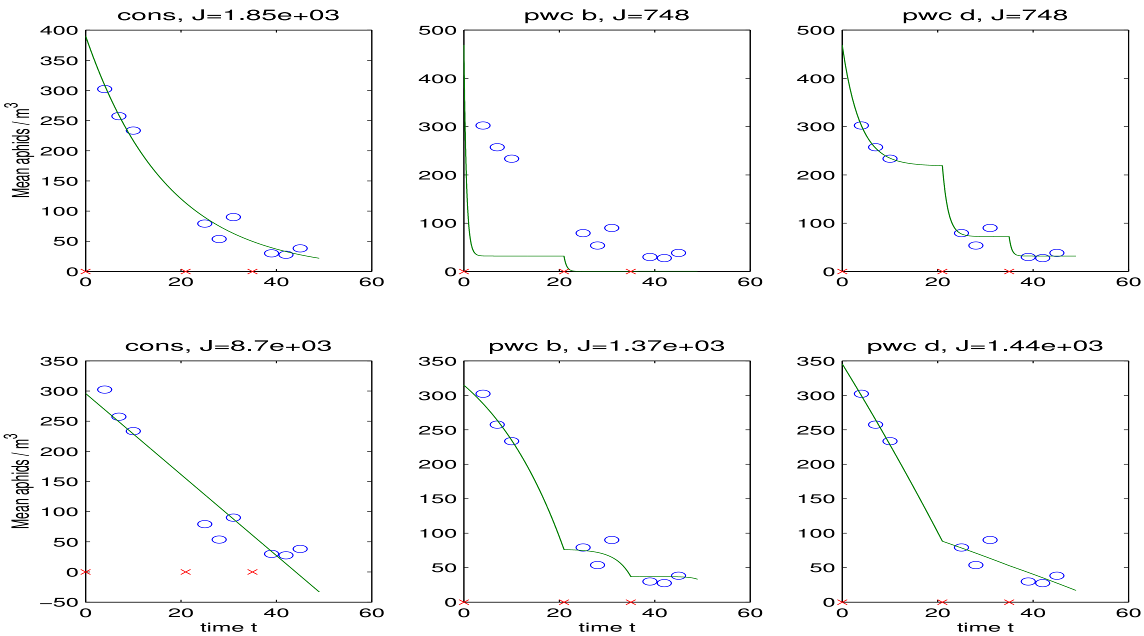

Figure 28: Fit of **Models 4 and 5** to data from **weedy margin, low spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, again with results for constant and **piecewise constant** coefficients.

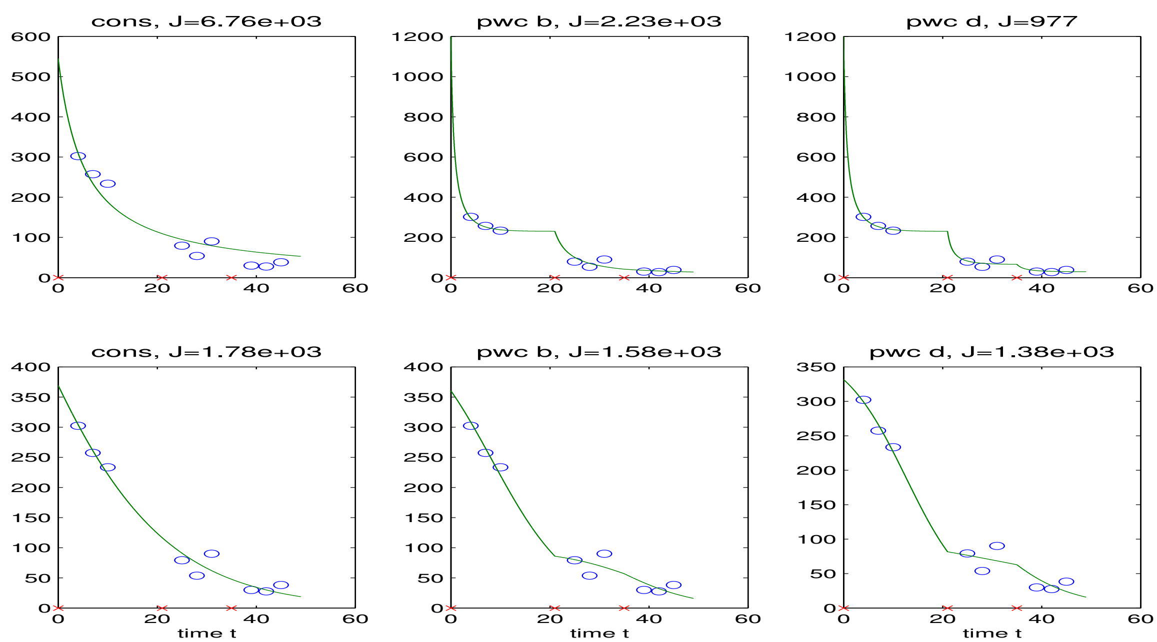

Figure 29: Fit of **logistic Models 6 and 7** to data from **weedy margin, low spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN^2 - dN$, again with results for constant coefficients and **piecewise constant** coefficients.

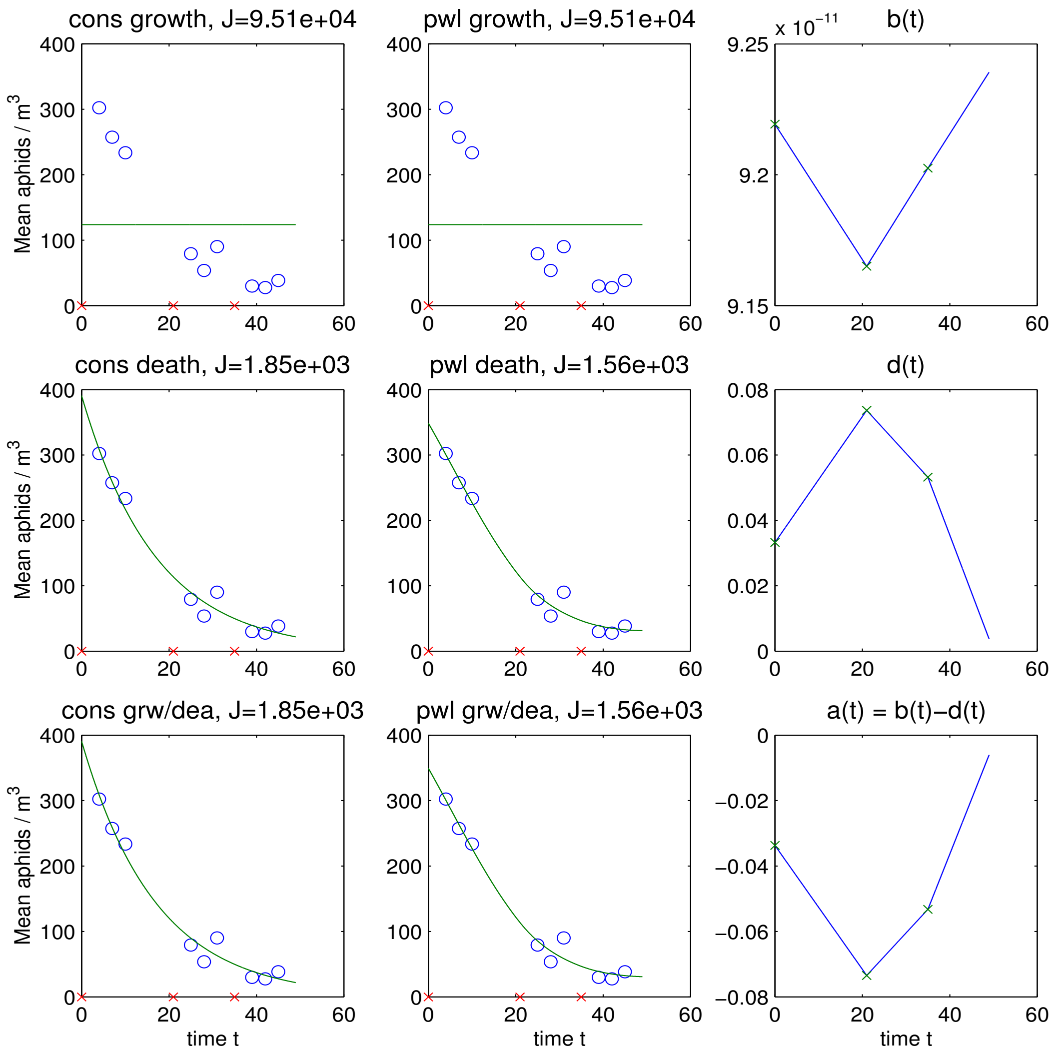

Figure 30: Fit of **exponential models** to data from **weedy margin, low spray**. Coefficients are either constant (left column) or **piecewise linear** (center column) and pwl coefficients are shown in the right column. Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

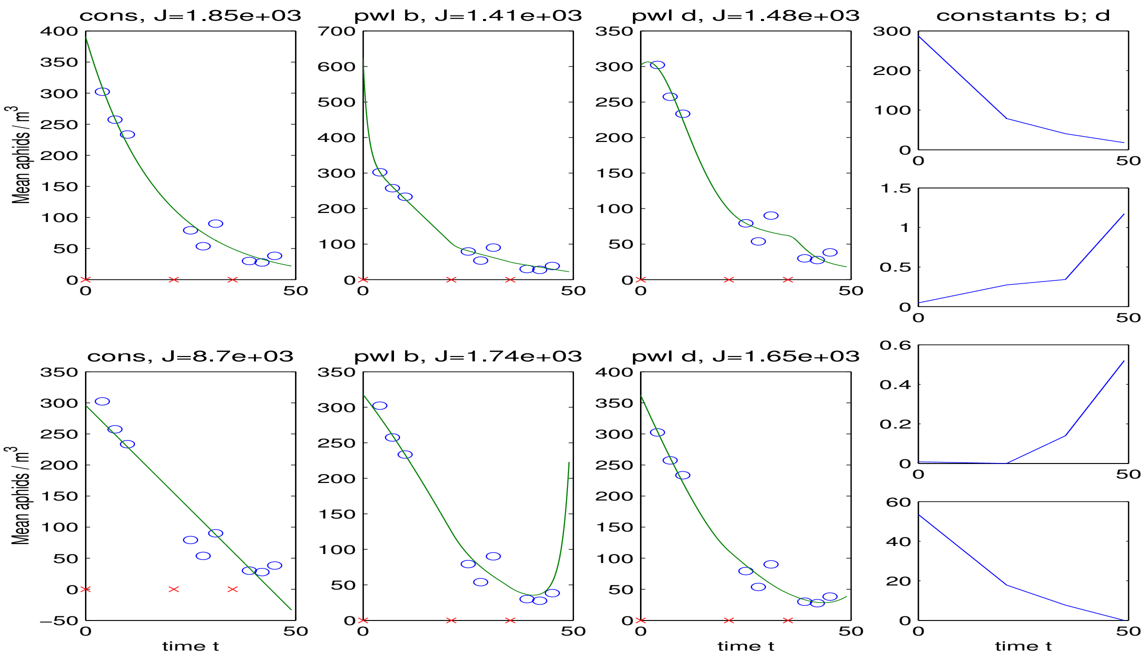

Figure 31: Fit of **Models 4 and 5** to data from **weedy margin, low spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, **piecewise linear** coefficient $d(t)$, and the resulting coefficients from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, with the same columns.

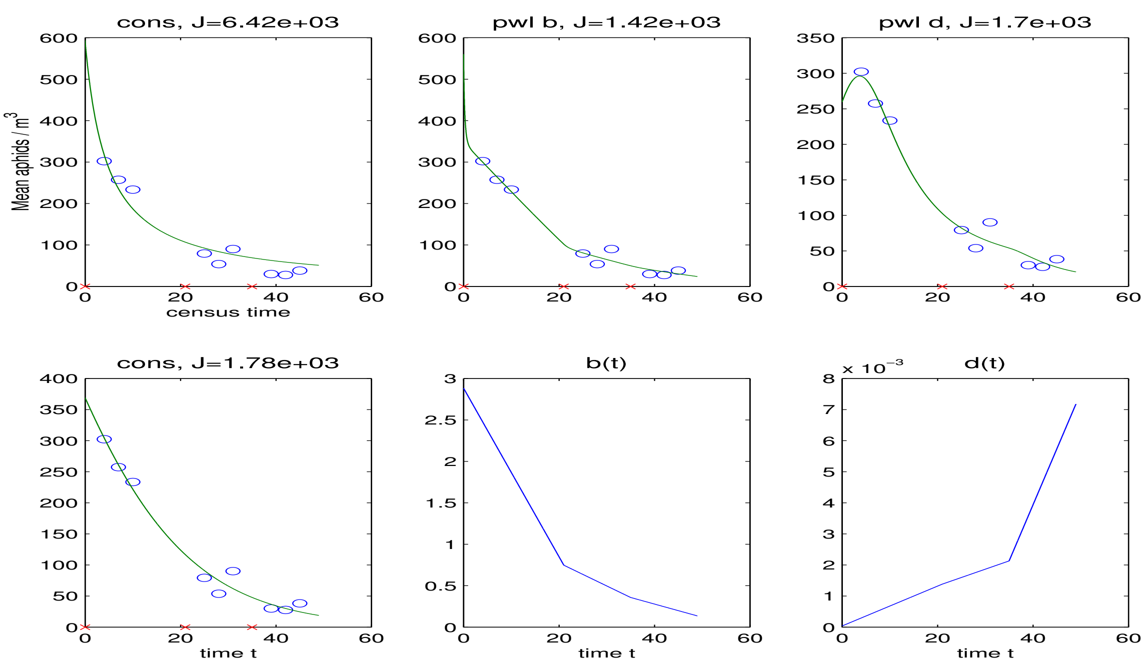

Figure 32: Fit of **logistic Model 6** to data from **weedy margin, low spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, and **piecewise linear** coefficient $d(t)$ from left to right. Row 2 shows the resulting coefficients.

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	J	9.5130e+04	1.8532e+03	1.8532e+03	1.8532e+03	8.7019e+03	6.7551e+03	1.7755e+03
pwc $b(t)$	J	9.5130e+04	n/a	1.8312e+03	7.4849e+02	1.3656e+03	2.2279e+03	1.5789e+03
	U	0.00		0.11	13.28	48.35	18.29	1.12
	$1-\alpha$	0.000		0.053	0.999	1.000	1.000	0.429
pwc $d(t)$	J	n/a	1.8312e+03	n/a	7.4849e+02	1.4425e+03	9.7652e+02	1.3795e+03
	U		0.11		13.28	45.29	53.26	2.58
	$1-\alpha$		0.053		0.999	1.000	1.000	0.725
cons	J	9.5130e+04	1.8532e+03	1.8532e+03	1.8532e+03	8.7019e+03	6.4203e+03	–
pwl $b(t)$	J	9.5130e+04	n/a	1.5607e+03	1.4132e+03	1.7449e+03	1.4158e+03	–
	U	0.00		1.69	2.80	35.88	31.81	
	$1-\alpha$	0.000		0.360	0.577	1.000	1.000	
pwl $d(t)$	J	n/a	1.5603e+03	n/a	1.4831e+03	1.6453e+03	1.6980e+03	–
	U		1.69		2.25	38.60	25.03	
	$1-\alpha$		0.361		0.477	1.000	1.000	

Table 11: Weedy margin, low spray: Summary of cost function values and statistics.

Comments

- This dataset essentially exhibits an exponential decay trend, so the simpler models fit well.
- As expected, the exponential birth model fails to fit the data at all, regardless of incorporation of time-varying coefficients. The exponential death model performs better and we do not observe any substantial improvement by using time-varying coefficients. Since the data trend is essentially decaying, we do not see any improvement by allowing birth and death, that is, Model 3 does not outperform Model 2.
- Of the remaining models, Model 4 yields the best fit to data, when considered with piecewise constant coefficients. Unfortunately while the residual is smaller, the initial condition estimated seems too large.
- There is no clear difference between allowing $b(t)$ versus $d(t)$ to be time-varying; their performance varies from model to model.
- For Models 5 and 6, we observe statistically significant improvement when adding any kind of time-varying coefficients, though to the naked eye, the fits offered by these models are not appreciably better.
- In increasing order of least squares residual, the top models are: Model 4 (pwc b or d); Model 6 (pwc d); Model 5 (pwc b); and Model 7 (pwc d). Notice that for this dataset, piecewise constant coefficients outperformed piecewise linear.

5.6 Dataset 6: Weedy margin, high spray (30 g ai/ha)

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	$b \mid a$	3.9640e-12	n/a	-4.5290e-02	3.0840e-08	2.7641e-03	2.2880e-09	6.8835e-04
	d	n/a	4.5293e-02	n/a	4.5291e-02	6.0575e+00	2.9001e-04	1.6296e-01
	N_0	110	293	293	293	254	317	233
	J	8.2011e+04	2.4298e+04	2.4298e+04	2.4298e+04	1.9209e+04	3.2758e+04	1.6269e+04
pwc $b(t)$ or $a(t)$	$b_1 \mid a_1$	1.9826e-13	n/a	3.3172e-02	9.5504e+01	1.3023e-01	2.5470e+00	6.9557e-04
	$b_2 \mid a_2$	1.9825e-13		-2.5439e-01	2.5391e+01	3.0482e-01	8.5426e-01	1.0468e-03
	$b_3 \mid a_3$	1.9820e-13		4.7344e-02	3.6168e+00	6.7097e-01	4.7069e-02	1.0019e-08
	d	n/a		n/a	3.7390e-01	3.0836e+01	1.0053e-02	1.6594e-01
	N_0	110		178	0	228	0	233
	J	8.2011e+04		1.5697e+04	8.7178e+03	1.6539e+04	7.4339e+03	1.6101e+04
	U	0.00		4.93	16.08	1.45	30.66	0.09
	$1-\alpha$	0.000		0.915	1.000	0.516	1.000	0.046
pwc $d(t)$	b	n/a	n/a	n/a	5.5139e+01	2.0740e-01	2.4627e-01	1.4429e-03
	d_1		2.4424e-10		1.5014e-01	4.8190e+01	6.1679e-04	3.3658e-01
	d_2		1.4477e-01		7.2576e-01	2.1303e+01	3.6529e-03	1.0053e-01
	d_3		9.0940e-02		3.5003e+00	7.3246e+00	1.9148e-02	4.9900e-01
	N_0		223		0	231	78	233
	J		1.6478e+04		4.1709e+03	1.3731e+04	3.9552e+03	1.2203e+04
	U		4.27		43.43	3.59	65.54	3.00
	$1-\alpha$		0.882		1.000	0.834	1.000	0.777
cons	$b \mid a$	3.3403e-09	n/a	-4.5308e-02	3.3257e-05	2.8135e-03	3.0535e-08	–
	d	n/a	4.5293e-02	n/a	4.5226e-02	6.0636e+00	2.9061e-04	
	N_0	110	293	293	293	254	318	
	J	8.2011e+04	2.4298e+04	2.4298e+04	2.4298e+04	1.9209e+04	3.2745e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	1.6722e-10	n/a	2.3849e-01	5.9473e+01	7.7733e-02	4.3605e-01	–
	$b_2 \mid a_2$	1.6815e-10		-1.8197e-01	5.7922e-03	6.2092e-08	7.0637e-09	
	$b_3 \mid a_3$	1.6769e-10		2.4690e-01	5.8771e-01	1.4964e-01	4.8039e-09	
	$b_4 \mid a_4$	1.6702e-10		-5.0000e+00	8.5440e-02	9.0937e-01	1.4877e-08	
	d	n/a		n/a	1.0457e-01	1.2653e+01	8.3158e-04	
	N_0	110		73	0	224	43	
	J	8.2011e+04		3.1240e+03	8.0410e+03	1.4054e+04	8.6399e+03	
	U	0.00		61.00	18.20	3.30	25.11	
	$1-\alpha$	0.000		1.000	1.000	0.653	1.000	
pwl $d(t)$	b	n/a	n/a	n/a	4.7187e+01	8.6835e-02	2.3836e-01	–
	d_1		7.3573e-09		3.6083e-06	4.7379e-04	1.0233e-08	
	d_2		5.9863e-02		4.0225e-01	3.5030e+01	1.8417e-03	
	d_3		5.1267e-09		7.2455e-01	3.9276e+00	5.3865e-03	
	d_4		2.3402e+00		7.1127e+00	5.6363e+00	5.7089e-02	
	N_0		239		1	151	66	
	J		1.6479e+04		7.4452e+03	1.1752e+04	7.4899e+03	
	U		4.27		20.37	5.71	30.35	
	$1-\alpha$		0.766		1.000	0.873	1.000	

Table 12: Weedy margin, high spray: Optimal parameters and cost for constant versus piecewise constant coefficients for all models (top) and constant versus piecewise linear coefficients (bottom) for Models 1–6.

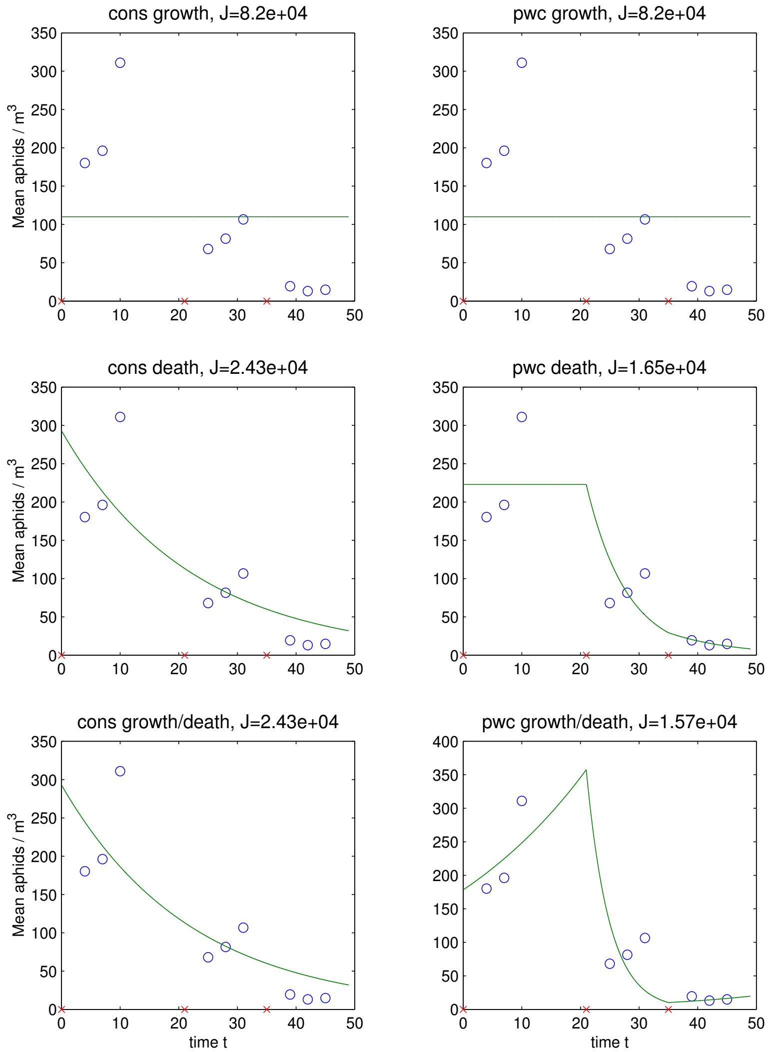

Figure 33: Fit of **exponential models** to data from **weedy margin, high spray**. Coefficients are either constant (left column) or **piecewise constant** (right column). Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

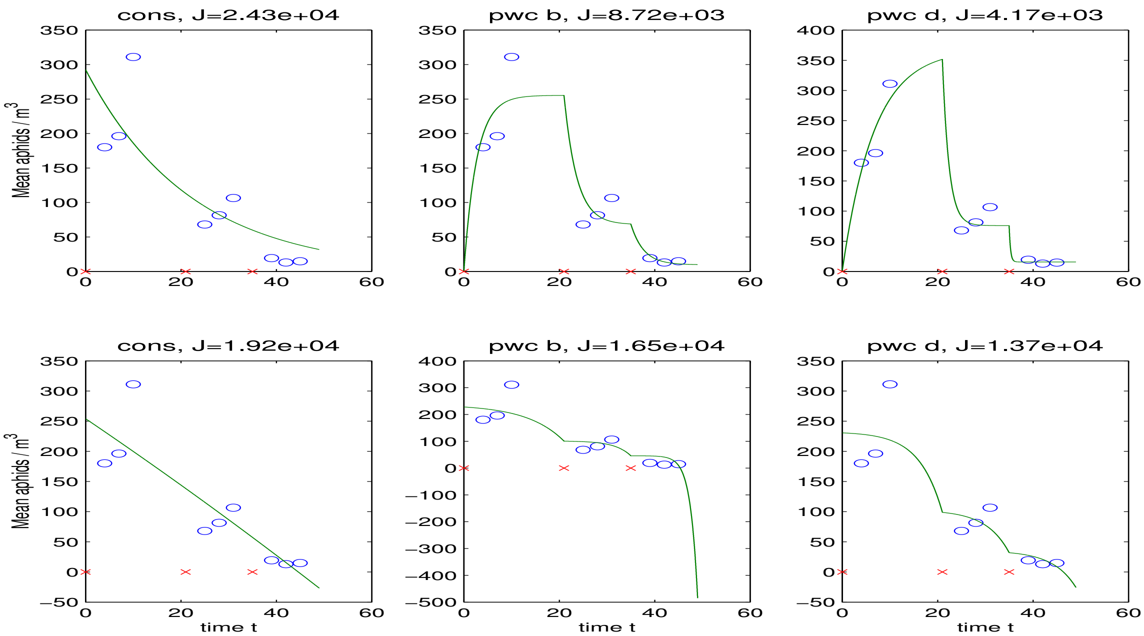

Figure 34: Fit of **Models 4 and 5** to data from **weedy margin, high spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, again with results for constant and **piecewise constant** coefficients.

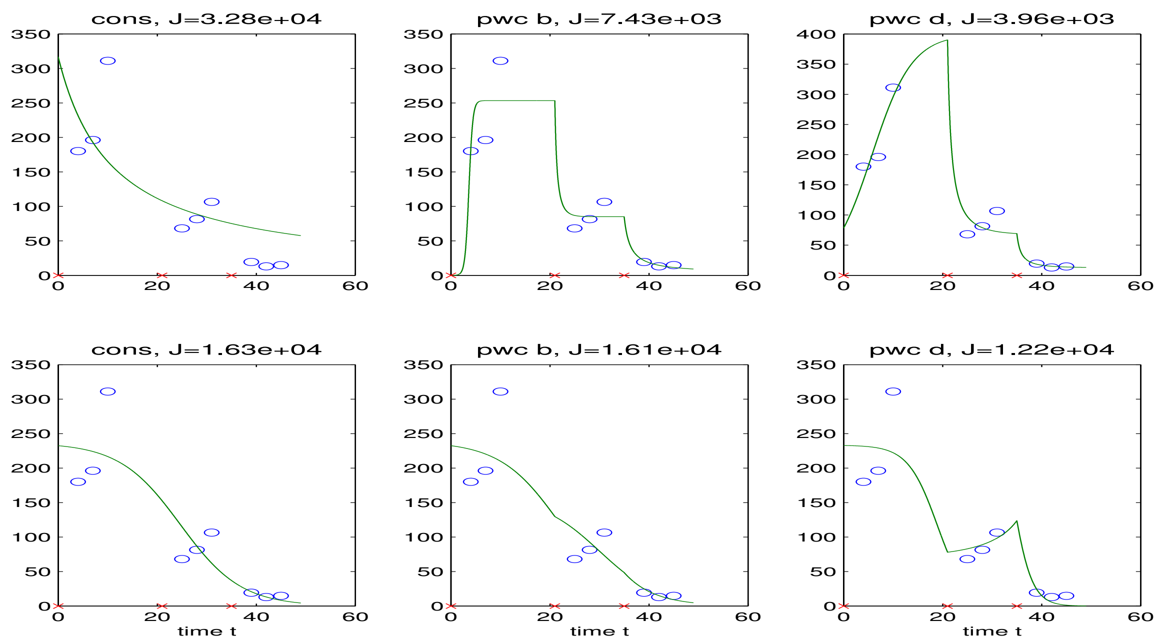

Figure 35: Fit of **logistic Models 6 and 7** to data from **weedy margin, high spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise constant** coefficient $b(t)$, and **piecewise constant** coefficient $d(t)$ from left to right. Row 2 corresponds to the model $\dot{N} = bN^2 - dN$, again with results for constant coefficients and **piecewise constant** coefficients.

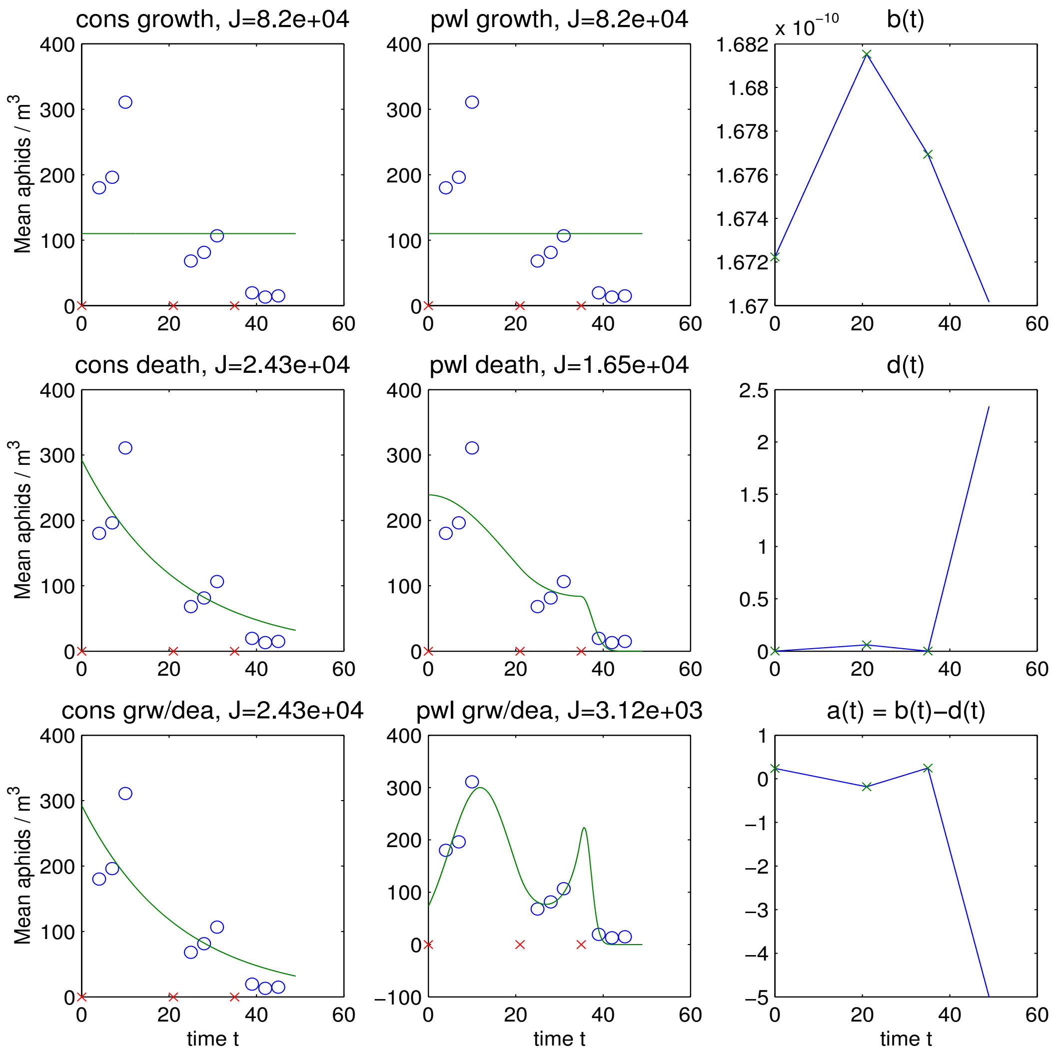

Figure 36: Fit of **exponential models** to data from **weedy margin, high spray**. Coefficients are either constant (left column) or **piecewise linear** (center column) and pwl coefficients are shown in the right column. Rows 1–3 correspond to exponential Models 1–3, respectively (birth, death, combined birth/death).

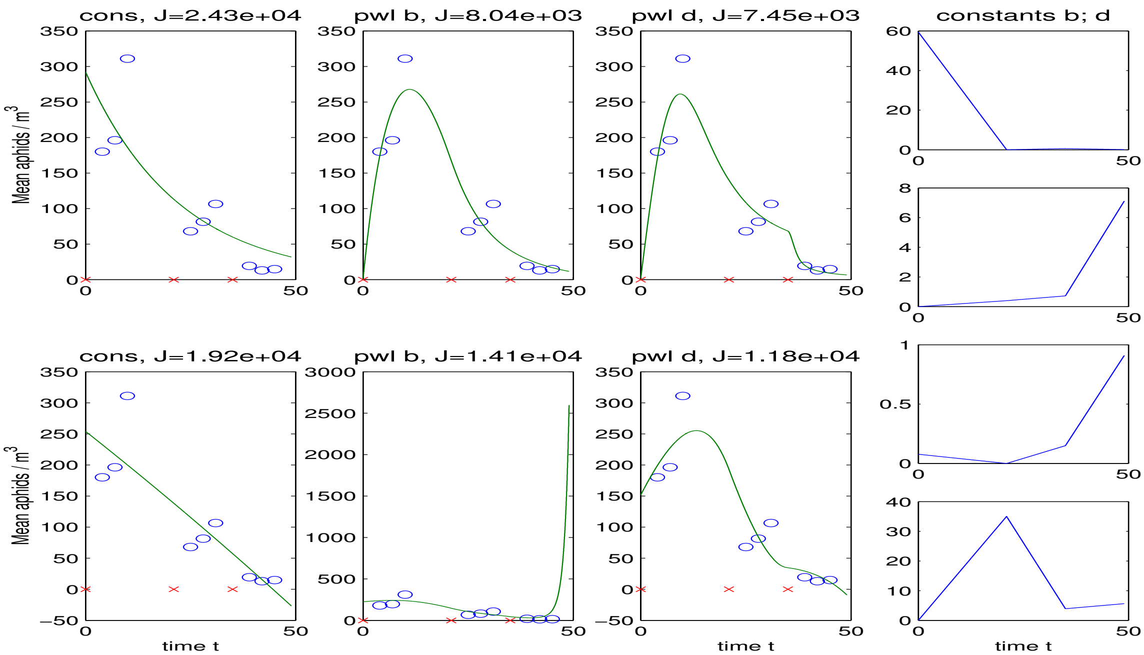

Figure 37: Fit of **Models 4 and 5** to data from **weedy margin, high spray**. Row 1 corresponds to the model $\dot{N} = b - dN$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, **piecewise linear** 7coefficient $d(t)$, and the resulting coefficients from left to right. Row 2 corresponds to the model $\dot{N} = bN - d$, with the same columns.

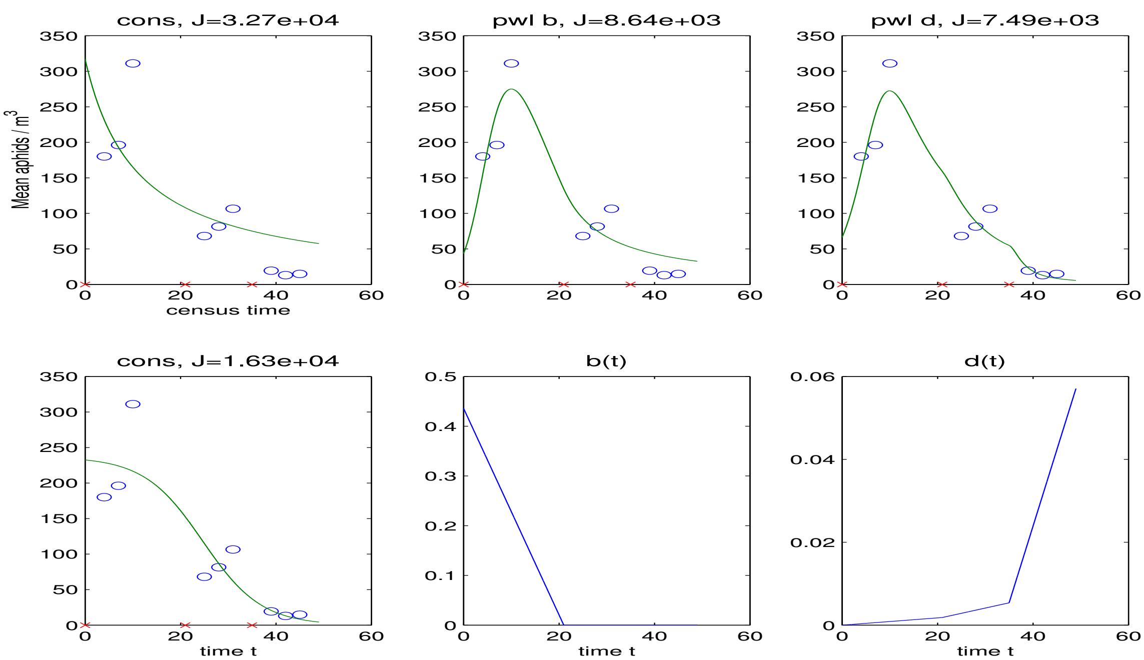

Figure 38: Fit of **logistic Model 6** to data from **weedy margin, high spray**. Row 1 corresponds to the model $\dot{N} = bN - dN^2$, with results for constant coefficients, **piecewise linear** coefficient $b(t)$, and **piecewise linear** coefficient $d(t)$ from left to right. Row 2 shows the resulting coefficients.

coeff type	var	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
		$\dot{N} = bN$	$\dot{N} = -dN$	$\dot{N} = aN\,(a \in \mathbb{R})$	$\dot{N} = b - dN$	$\dot{N} = bN - d$	$\dot{N} = bN - dN^2$	$\dot{N} = bN^2 - dN$
cons	J	8.2011e+04	2.4298e+04	2.4298e+04	2.4298e+04	1.9209e+04	3.2758e+04	1.6269e+04
pwc $b(t)$	J	8.2011e+04		1.5697e+04	8.7178e+03	1.6539e+04	7.4339e+03	1.6101e+04
	U	0.00	n/a	4.93	16.08	1.45	30.66	0.09
	$1-\alpha$	0.000		0.915	1.000	0.516	1.000	0.046
pwc $d(t)$	J		1.6478e+04		4.1709e+03	1.3731e+04	3.9552e+03	1.2203e+04
	U	n/a	4.27	n/a	43.43	3.59	65.54	3.00
	$1-\alpha$		0.882		1.000	0.834	1.000	0.777
cons	J	8.2011e+04	2.4298e+04	2.4298e+04	2.4298e+04	1.9209e+04	3.2745e+04	–
pwl $b(t)$	J	8.2011e+04		3.1240e+03	8.0410e+03	1.4054e+04	8.6399e+03	
	U	0.00	n/a	61.00	18.20	3.30	25.11	–
	$1-\alpha$	0.000		1.000	1.000	0.653	1.000	
pwl $d(t)$	J		1.6479e+04		7.4452e+03	1.1752e+04	7.4899e+03	
	U	n/a	4.27	n/a	20.37	5.71	30.35	–
	$1-\alpha$		0.766		1.000	0.873	1.000	

Table 13: Weedy margin, high spray: Summary of cost function values and statistics.

Comments

- Again, the exponential birth model fails to fit the data at all, regardless of incorporation of time-varying coefficients. The exponential death model also fails to fit the data.
- Model 3 (exponential birth/death) with piecewise linear time-varying coefficients is the best-fitting model and their incorporation is statistically significant at the 99% confidence level.
- Models 5 and 7 fit well, even with constant coefficients. We see some discrepancy between the constant coefficient solutions computed with the ODE solver versus with the analytical solution.
- In general the solution curves at the optimal parameters seem more erratic for this dataset, especially for piecewise constant coefficients, where there are a lot of abrupt changes in trajectory.
- Of the remaining models, Models 4 and 6 leave the smallest residuals and adding any kind of time-varying coefficients is statistically significant at the 99% confidence level.
- The model ranking for this dataset is: Model 3 (pwl); Model 6 (pwc d); Model 4 (pwc d); Model 6 (pwc b) ; Model 4 (pwl d); and Model 6 (pwl d). We again observe that time-varying $d(t)$ are often better than $b(t)$.

6 Standard error results

6.1 Results for fits from Section 5

Tables 14 through 19 show the standard errors (estimates of variance) for parameters in Models 3 and 6, for datasets 1 through 6. We focus on these two models (especially with piecewise linear coefficients) to demonstrate the computational method since they are of greatest interest to us following our initial parameter estimation. Computations are as described in Section 4.3 and the sensitivity equations are solved with ODE solver relative tolerance 10^{-6} and absolute tolerance 10^{-9}. Observe that while in many cases the standard errors are reasonable, we see from Tables 16, 17, and 18, that in many cases there are substantial variances. This is somewhat to be expected, since in some cases we estimate six parameters in a dynamical model using only nine data points. Further exploration of this phenomenon is detailed in Section 6.2.

coeff type	var	Model 3 ($\dot{N} = aN$ ($a \in \mathbb{R}$)) μ	Model 3 σ	Model 6 ($\dot{N} = bN - dN^2$) μ	Model 6 σ
cons	$b \mid a$	-1.1919e-02	4.7231e-03	4.8430e-07	1.0157e-01
	d	n/a	n/a	3.6550e-05	3.3912e-04
	N_0	395	47	394	97
	J	2.6554e+04		2.8333e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	1.1232e-01	6.1365e-02	1.5264e-01	5.7836e-01
	$b_2 \mid a_2$	-4.3865e-02	2.4033e-02	1.1703e-02	7.3569e-01
	$b_3 \mid a_3$	-2.8820e-02	3.2907e-02	2.2547e-04	3.8509e-01
	$b_4 \mid a_4$	7.4932e-03	1.3094e-01	2.9598e-02	4.0528e-01
	d	n/a	n/a	1.2550e-04	1.7081e-03
	N_0	199	70	189	176
	J	1.0123e+04	n/a	1.0193e+04	n/a
	U	14.61		16.02	
	$1-\alpha$	0.998		0.999	
pwl $d(t)$	b	n/a	n/a	1.1665e-01	7.6459e-01
	d_1			4.0952e-07	2.2608e-03
	d_2			3.8839e-04	1.7837e-03
	d_3			5.8297e-04	3.1548e-03
	d_4			6.4757e-04	3.9804e-03
	N_0			184	216
	J			1.0220e+04	n/a
	U			15.95	
	$1-\alpha$			0.999	

Table 14: **Bare margin, no spray:** initial parameter estimates μ and standard errors σ for Models 3 and 6.

coeff type	var	Model 3 ($\dot{N} = aN$ ($a \in \mathbb{R}$)) μ	Model 3 σ	Model 6 ($\dot{N} = bN - dN^2$) μ	Model 6 σ
cons	$b \mid a$	-3.0353e-03	9.3249e-03	4.6044e-01	1.5652e+00
	d	n/a	n/a	2.6087e-03	9.0260e-03
	N_0	181	48	48	248
	J	3.3400e+04		3.1560e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	1.3174e-01	1.8439e-01	3.9487e-01	7.6327e-01
	$b_2 \mid a_2$	-3.1967e-02	6.7396e-02	1.4407e-01	1.2224e+00
	$b_3 \mid a_3$	-1.5505e-02	7.4227e-02	1.2657e-01	8.3225e-01
	$b_4 \mid a_4$	-8.0707e-02	3.0998e-01	5.7718e-07	7.0874e-01
	d	n/a	n/a	7.9110e-04	4.9393e-03
	N_0	84	91	22	72
	J	2.1561e+04	n/a	1.8950e+04	n/a
	U	4.94		5.99	
	$1-\alpha$	0.824		0.888	
pwl $d(t)$	b	n/a	n/a	2.2110e-01	8.3003e-01
	d_1			1.1753e-08	4.8444e-03
	d_2			1.2122e-03	3.8138e-03
	d_3			1.0543e-03	4.2719e-03
	d_4			3.5480e-03	8.4937e-03
	N_0			44	114
	J			1.7237e+04	n/a
	U			7.48	
	$1-\alpha$			0.942	

Table 15: **Bare margin, low spray:** parameter estimates μ and standard errors σ for Models 3 and 6.

coeff type	var	Model 3 ($\dot{N} = aN$ ($a \in \mathbb{R}$)) μ	Model 3 σ	Model 6 ($\dot{N} = bN - dN^2$) μ	Model 6 σ
cons	$b \mid a$	-9.8693e-03	9.0441e-03	2.1707e-07	2.3784e-01
	d	n/a	n/a	5.0075e-05	1.3882e-03
	N_0	216	51	212	97
	J	3.2146e+04		3.2993e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	2.4836e-02	1.2227e-01	1.4878e-01	1.1950e+00
	$b_2 \mid a_2$	2.0486e-02	4.8434e-02	1.4464e-01	2.4078e+00
	$b_3 \mid a_3$	-1.0502e-01	6.7966e-02	7.9690e-07	1.3069e+00
	$b_4 \mid a_4$	1.1666e-01	2.7506e-01	6.0767e-02	5.4498e-01
	d	n/a	n/a	5.2798e-04	8.6817e-03
	N_0	154	104	114	134
	J	1.1290e+04	n/a	1.2420e+04	n/a
	U	16.62		14.91	
	$1-\alpha$	0.999		0.998	
pwl $d(t)$	b	n/a	n/a	4.4446e+00	1.9150e+02
	d_1			2.6468e-02	1.1440e+00
	d_2			1.9865e-02	8.5804e-01
	d_3			1.8867e-02	8.1184e-01
	d_4			8.9076e-02	3.7154e+00
	N_0			702	5.976877e+10
	J			1.1604e+04	n/a
	U			16.59	
	$1-\alpha$			0.999	

Table 16: **Bare margin, high spray:** parameter estimates μ and standard errors σ for Models 3 and 6. Observe unreasonably high variance for N_0 in the Model 6 piecewise linear $d(t)$ case. Several other parameters have large standard errors, given the magnitude of the parameters.

coeff type	var	Model 3 ($\dot{N} = aN\ (a \in \mathbb{R})$) μ	Model 3 σ	Model 6 ($\dot{N} = bN - dN^2$) μ	Model 6 σ
cons	$b \mid a$	-2.1539e-02	7.0853e-03	1.7204e-07	9.6265e-02
	d	n/a	n/a	6.9588e-05	3.5356e-04
	N_0	442	67	449	183
	J	4.5489e+04		5.3610e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	7.8328e-02	6.2520e-02	3.5225e+00	7.3590e+01
	$b_2 \mid a_2$	-2.7575e-02	2.5915e-02	5.0008e+00	1.0793e+02
	$b_3 \mid a_3$	-8.8266e-02	5.0496e-02	1.6283e+00	3.6084e+01
	$b_4 \mid a_4$	8.2007e-03	2.3207e-01	9.3088e-01	2.0112e+01
	d	n/a	n/a	1.0922e-02	2.3269e-01
	N_0	243	85	356	257222023
	J	1.1162e+04	n/a	1.2029e+04	n/a
	U	27.68		31.11	
	$1-\alpha$	1.000		1.000	
pwl $d(t)$	b	n/a	n/a	6.4854e-02	1.0874e+00
	d_1			1.4981e-08	3.3233e-03
	d_2			1.8816e-04	2.2235e-03
	d_3			6.9877e-04	5.2247e-03
	d_4			1.2667e-03	1.3773e-02
	N_0			253	201
	J			1.1223e+04	n/a
	U			33.99	
	$1-\alpha$			1.000	

Table 17: **Weedy margin, no spray:** parameter estimates μ and standard errors σ for Models 3 and 6. Observe unreasonably high variance for several parameters, and especially N_0, in the Model 6 piecewise linear $b(t)$ case.

coeff type	var	Model 3 ($\dot{N} = aN\ (a \in \mathbb{R})$) μ	Model 3 σ	Model 6 ($\dot{N} = bN - dN^2$) μ	Model 6 σ
cons	$b \mid a$	-5.8838e-02	4.6498e-03	1.8188e-08	3.2451e-02
	d	n/a	n/a	3.6553e-04	2.4914e-04
	N_0	391	20	594	318
	J	1.8532e+03		6.4203e+03	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	-3.3683e-02	3.3764e-02	2.8839e+00	8.7601e+01
	$b_2 \mid a_2$	-7.3455e-02	2.2960e-02	7.4802e-01	2.3807e+01
	$b_3 \mid a_3$	-5.3253e-02	6.7707e-02	3.5859e-01	1.2110e+01
	$b_4 \mid a_4$	-6.0475e-03	3.0246e-01	1.3565e-01	5.7342e+00
	d	n/a	n/a	8.3909e-03	2.5086e-01
	N_0	350	58	561	6317532
	J	1.5607e+03	n/a	1.4158e+03	n/a
	U	1.69		31.81	
	$1-\alpha$	0.360		1.000	
pwl $d(t)$	b	n/a	n/a	8.0585e-02	5.0905e-01
	d_1			3.6872e-05	7.2195e-04
	d_2			1.3836e-03	4.5713e-03
	d_3			2.1305e-03	1.0089e-02
	d_4			7.1794e-03	2.1254e-02
	N_0			259	252
	J			1.6980e+03	n/a
	U			25.03	
	$1-\alpha$			1.000	

Table 18: **Weedy margin, low spray:** parameter estimates μ and standard errors σ for Models 3 and 6. Again, observe unreasonably high variance for N_0 (and other parameters) in the piecewise linear $b(t)$ case for Model 6.

coeff type	var	Model 3 ($\dot{N} = aN$ ($a \in \mathbb{R}$)) μ	Model 3 σ	Model 6 ($\dot{N} = bN - dN^2$) μ	Model 6 σ
cons	$b \mid a$	-4.5308e-02	1.5274e-02	3.0535e-08	1.0480e-01
	d	n/a	n/a	2.9061e-04	8.9634e-04
	N_0	293	63	318	301
	J	2.4298e+04		3.2745e+04	
pwl $b(t)$ or $a(t)$	$b_1 \mid a_1$	2.3849e-01	6.1702e-02	4.3605e-01	6.8975e-01
	$b_2 \mid a_2$	-1.8197e-01	4.3079e-02	7.0637e-09	3.5514e-01
	$b_3 \mid a_3$	2.4690e-01	1.7799e-01	4.8039e-09	2.0463e-01
	$b_4 \mid a_4$	-5.0000e+00	3.0198e+00	1.4877e-08	7.7309e-01
	d	n/a	n/a	8.3158e-04	2.3423e-03
	N_0	73	25	43	98
	J	3.1240e+03	n/a	8.6399e+03	n/a
	U	61.00		25.11	
	$1-\alpha$	1.000		1.000	
pwl $d(t)$	b	n/a	n/a	2.3836e-01	6.0735e-01
	d_1			1.0233e-08	2.5834e-03
	d_2			1.8417e-03	3.1529e-03
	d_3			5.3865e-03	1.3270e-02
	d_4			5.7089e-02	1.6867e-01
	N_0			66	110
	J			7.4899e+03	n/a
	U			30.35	
	$1-\alpha$			1.000	

Table 19: **Weedy margin, high spray:** parameter estimates μ and standard errors σ for Models 3 and 6.

6.2 Further exploration of variance

To try to better understand the large variances seen in our parameter estimates, especially with Model 6, we experiment with the datasets corresponding to bare ground, high spray and weedy ground, no spray, re-running the inverse problem with two factors:

1. *Estimating only a subset of the parameters at a time.* Attempted with Models 3 and 6.

2. *Further restricting the admissible parameter set from which the optimal q can be chosen.* Prompted by some odd-looking fits to data, as well as unreasonable parameters and initial conditions, we study the effect of this factor on the results for Model 6.

We also tighten the ODE solver relative tolerance for the inverse problem forward solves to 10^{-4} to ensure accuracy in the variance computations.

Estimation experiments with Model 3 ($\dot{N} = aN$)

In fitting Model 3, we do not observe any wildly deviant parameter values or initial conditions, so we only study factor 1: the effect of estimating a subset of parameters. After estimating parameters in the constant coefficient case, we estimate (a) all five parameters in the piecewise linear coefficient variant of Model 3, then (b) only a_1 – a_4 (holding N_0 at the previously estimated optimal value), and (c) only N_0, holding a_1 – a_4 at previous optimal values.

There is no perceivable difference in fit in estimating over all the parameters or some restricted parameter set (see Figures 39 and 40). For the bare ground, high spray case, we observe substantial reduction in variance when estimating either subset of the parameters (see Table 20). So if we had reasonable estimates of either $a_1 - a_4$ or N_0 and could estimate only the other parameter(s), we could expect smaller variance in the estimates. From Table 21 we observe that for the weedy ground, no spray case, there is a small difference in estimating $a(t)$ only and a more substantial reduction in variance when estimating only N_0.

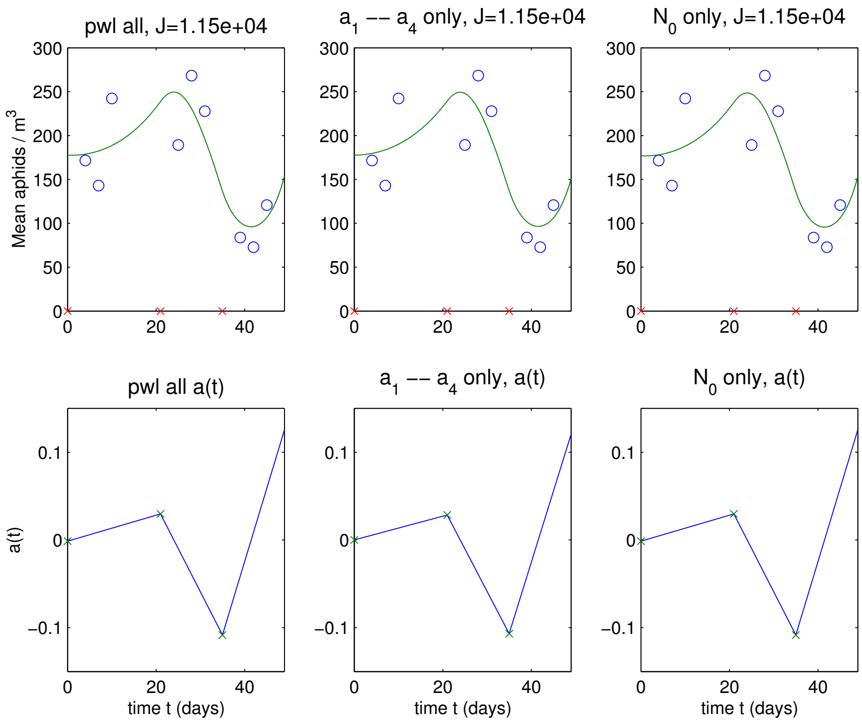

Figure 39: **Bare ground, high spray:** Comparison of fit and piecewise linear coefficients for fitting all parameters (column 1), only $a_1 - a_4$ (column 2), or only N_0 (column 3) in Model 3. When optimizing over a restricted parameter set, all other parameters are kept at the optimal values from estimating them all simultaneously. Notice all fits are nearly identical and estimated time-varying parameters only vary slightly.

coeff type	var	Model 3 ($\dot{N} = aN$ ($a \in \mathbb{R}$)) μ	σ	Model 3 ($a(t)$ only) μ	σ	Model 3 (N_0 only) μ	σ
cons	a	-9.8693e-03	9.0441e-03				
	N_0	216	51				
	J	3.2146e+04					
pwl $a(t)$	a_1	-1.4269e-03	1.2171e-01	5.8145e-06	3.0460e-02	-1.4269e-03	
	a_2	2.9628e-02	4.9035e-02	2.8393e-02	2.5984e-02	2.9628e-02	
	a_3	-1.0830e-01	6.8443e-02	-1.0678e-01	5.8691e-02	-1.0830e-01	
	a_4	1.2543e-01	2.7512e-01	1.2054e-01	2.4311e-01	1.2543e-01	
	N_0	178	117	178		177	13
	J	1.1505e+04		1.1498e+04		1.1500e+04	
	U	16.15	n/a	16.16	n/a	16.16	n/a
	$1-\alpha$	0.999		0.999		0.999	

Table 20: **Bare ground, high spray:** Estimated parameters μ and standard errors σ for Model 3, estimating all parameters and select subsets of parameters. Notice reduction in standard error when estimating a subset of the parameters in both cases.

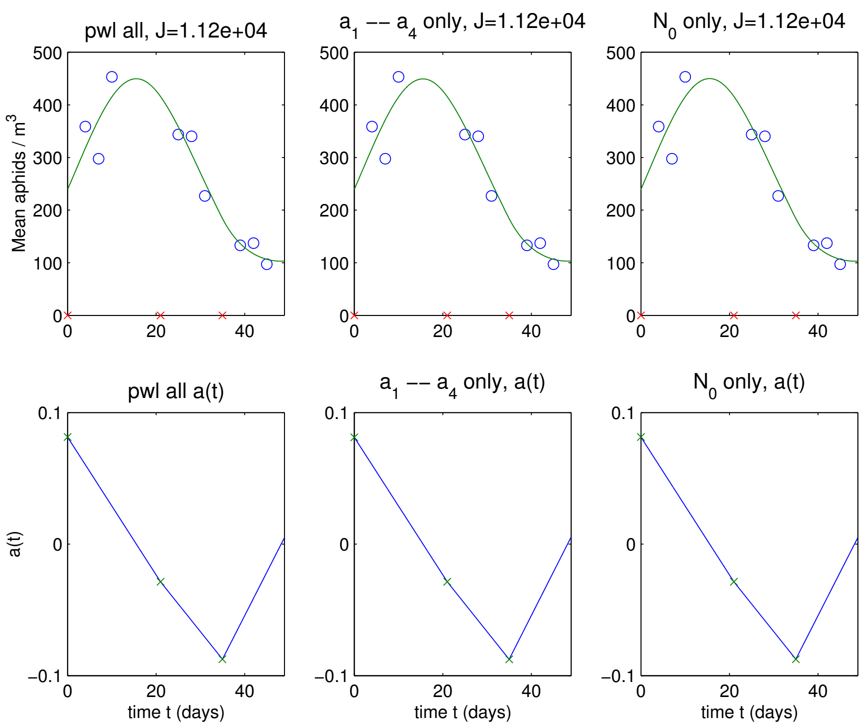

Figure 40: **Weedy ground, no spray:** Comparison of fit and piecewise linear coefficients for fitting all parameters (column 1), only $a_1 - a_4$ (column 2), or only N_0 (column 3) in Model 3. When optimizing over a restricted parameter set, all other parameters are kept at the optimal values from estimating them all simultaneously. Again, notice all fits are nearly identical and estimated parameters only vary slightly.

coeff type	var	Model 3 ($\dot{N} = aN$ ($a \in \mathbb{R}$)) μ	σ	Model 3 ($a(t)$ only) μ	σ	Model 3 (N_0 only) μ	σ
cons	a	-2.1539e-02	7.0853e-03				
	N_0	442	67				
	J	4.5489e+04					
pwl $a(t)$	a_1	8.1381e-02	6.2678e-02	8.1258e-02	1.4755e-02	8.1381e-02	
	a_2	-2.8643e-02	2.5924e-02	-2.8562e-02	1.4681e-02	-2.8643e-02	
	a_3	-8.7493e-02	5.0484e-02	-8.7602e-02	4.4103e-02	-8.7493e-02	
	a_4	4.9259e-03	2.3264e-01	5.3782e-03	2.0671e-01	4.9259e-03	
	N_0	239	84	239		239	10
	J	1.1180e+04	n/a	1.1180e+04	n/a	1.1180e+04	n/a
	U	27.62		27.62		27.62	
	$1-\alpha$	1.000		1.000		1.000	

Table 21: **Weedy ground, no spray:** Estimated parameters μ and standard errors σ for Model 3, estimating all parameters and select subsets of parameters. Notice more drastic reduction in standard error when estimating only N_0.

So as anticipated, there is reduction in variance when estimating fewer parameters, but some caution is necessary in interpreting this result. While we only estimate a subset of the parameters for this experiment, we hold one or more parameters at previously estimated *optimal* values. So at some point each of the five parameter values is actually estimated. This needs to be considered when assessing the uncertainty in the parameters.

Estimation experiments with Model 6 ($\dot{N} = bN - dN^2$)

We examine fitting Model 6 to the same two datasets, exploring both factors 1 and 2. First we estimate all six parameters in the model for the piecewise linear $b(t)$ and piecewise linear $d(t)$ cases. We then perform the same optimization with tighter bounds on the parameters, since some of the estimated parameters reported in Section 5 may not make physical sense (e.g., instantaneous growth rate of $b = 4.4$, in one case). We consider restricting the parameters according to the following table, where the limits on the parameters are [lower bound, upper bound]. For each of the cases original (reg.) bounds and restricted (tgt.) bounds, we

	bare margin, high spray		**weedy margin, no spray**	
	original	restricted	original	restricted
b	[1e-9, 5]	[1e-5, 1]	[1e-9, 10]	[1e-5, 1]
d	[1e-8, 1]	[1e-5, 0.1]	[1e-8, 1]	[1e-5, 0.1]
N_0	[0 , 1200]	[0, 500]	[0, 1200]	[0,600]

calculate standard errors for estimating all parameters, and then subsets of parameters. For example, we estimate $b_1 - b_4$, holding d, N_0 fixed at optimal, then vice-versa.

See Table 22 for the bare ground, high spray and Table 23 for the weedy ground, no spray, detailed results. Most of the model fits to data are nearly identical, so only a few select figures are included and referenced in the text below. In some cases tightening the bounds on the parameters substantially reduces variance. We see some reduction in variance by estimating fewer parameters, but have the same concerns as expressed above for Model 3.

Focusing on Table 22 (bare margin, high spray) we note that the piecewise linear $b(t)$ case does not exhibit reduction in variance when tightening parameter bounds, but does when estimating a subset of the parameters. In the piecewise linear $d(t)$ case, we see more significant reduction by estimating with tighter constraints and by reducing the number of free variables. Estimating only N_0 made a substantial difference in the fit in this latter case, though the variance estimate is still huge. Figure 41 illustrates a typical difference in fit obtained by tightening the bounds on the parameters. Visual fit to the data did not change appreciably for estimating subsets of parameters, so those plots are omitted.

Examining some sample plots for weedy margin, no spray (Figure 42, we see that the restriction of parameters helped significantly in the piecewise linear $b(t)$ case, smoothing the fit as shown in Figure 42. We do not see any visible difference in fit when estimating with a reduced parameter set, so the plots are omitted . We also observe that in some cases, the variance is still enormous, despite the incorporation of our two study factors (see Table 23).

coeff type	var	all free reg. bds. μ	all free reg. bds. σ	all free tgt. bds. μ	all free tgt. bds. σ	pwl free reg. bds. μ	pwl free reg. bds. σ	pwl free tgt. bds. μ	pwl free tgt. bds. σ	cons free reg. bds. μ	cons free reg. bds. σ	cons free tgt. bds. μ	cons free tgt. bds. σ
cons	b	9.9944e-07	2.3519e-01	1.1407e-05	2.3891e-01								
	d	5.0595e-05	1.3714e-03	4.9937e-05	1.3951e-03								
	N_0	213	97	212	96								
	J	3.2994e+04	3.2994e+04										
pwl $b(t)$	b_1	1.5575e-01	1.1982e+00	1.5425e-01	1.1690e+00	1.5560e-01	4.0994e-02	1.5462e-01	4.1070e-02	1.5575e-01		1.5425e-01	
	b_2	1.5063e-01	2.4711e+00	1.5197e-01	2.4142e+00	1.5044e-01	3.5699e-02	1.5176e-01	3.5785e-02	1.5063e-01		1.5197e-01	
	b_3	9.4729e-06	1.3082e+00	1.4236e-05	1.2803e+00	6.8466e-05	7.6409e-02	1.4818e-05	7.6478e-02	9.4729e-06		1.4236e-05	
	b_4	7.0770e-02	5.6205e-01	7.2668e-02	5.5208e-01	6.8562e-02	2.6722e-01	7.0879e-02	2.6676e-01	7.0770e-02		7.2668e-02	
	d	5.4836e-04	8.8272e-03	5.5126e-04	8.6292e-03	5.4836e-04		5.5126e-04		5.4893e-04	5.7305e-05	5.5125e-04	5.7461e-05
	N_0	110	136	111	134	110		111		111	28	111	28
	J	1.2437e+04		1.2434e+04		1.2436e+04		1.2433e+04		1.2435e+04		1.2434e+04	
	U	14.88		14.88		14.88		14.88		14.88		14.88	
	$1-\alpha$	0.998		0.998		0.998		0.998		0.998		0.998	
pwl $d(t)$	b	4.4539e+00	1.8961e+02	5.0466e-01	2.9670e+00	4.4539e+00		5.0466e-01		4.4519e+00	3.6155e-01	5.0549e-01	3.6155e-01
	d_1	2.6362e-02	1.1255e+00	2.6427e-03	1.7064e-02	2.6490e-02	6.2864e-03	2.6441e-03	6.7894e-04	2.6362e-02		2.6427e-03	
	d_2	2.0113e-02	8.5863e-01	2.2269e-03	1.3359e-02	1.9965e-02	6.6032e-03	2.2224e-03	6.6882e-04	2.0113e-02		2.2269e-03	
	d_3	1.8668e-02	7.9402e-01	2.2239e-03	1.2754e-02	1.8851e-02	6.9097e-03	2.2235e-03	1.0583e-03	1.8668e-02		2.2239e-03	
	d_4	8.9878e-02	3.7029e+00	1.3213e-02	5.4532e-02	8.9294e-02	3.8018e-02	1.3338e-02	7.0246e-03	8.9878e-02		1.3213e-02	
	N_0	584	4.804537e+10	74	485	584		74		1090	1.071894e+11	74	72
	J	1.1601e+04		1.2711e+04		1.1598e+04		1.2708e+04		1.1600e+04		1.2709e+04	
	U	16.60		14.36		16.60		14.37		16.60		14.36	
	$1-\alpha$	0.999		0.998		0.999		0.998		0.999		0.998	

Table 22: **Bare margin, high spray:** Parameter estimates μ and variance σ for Model 6 with various constraints and subsets of parameters estimated.

coeff type	var	all free reg. bds.		all free tgt. bds.		pwl free reg. bds.		pwl free tgt. bds.		cons free reg. bds.		cons free tgt. bds.	
		μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ
cons	b	1.7204e-07	9.6278e-02	1.0587e-05	9.7411e-02								
	d	6.9579e-05	3.5361e-04	6.8878e-05	3.5824e-04								
	N_0	449	183	446	181								
	J	5.3610e+04	5.3636e+04										
pwl $b(t)$	b_1	5.4480e+00	1.5385e+02	2.1974e-01	1.7821e+00	5.4602e+00	8.5151e-01	2.1978e-01	2.7051e-02	5.4480e+00		2.1974e-01	
	b_2	7.8745e+00	2.2670e+02	1.8475e-01	2.1429e+00	7.8541e+00	1.0948e+00	1.8473e-01	3.0385e-02	7.8745e+00		1.8475e-01	
	b_3	2.5248e+00	7.4086e+01	1.1751e-05	9.6535e-01	2.5362e+00	1.0070e+00	1.0222e-05	6.3221e-02	2.5248e+00		1.1751e-05	
	b_4	1.5226e+00	4.3653e+01	2.7275e-02	3.6669e-01	1.5208e+00	1.3341e+00	2.6962e-02	2.2859e-01	1.5226e+00		2.7275e-02	
	d	1.7050e-02	4.8694e-01	4.8060e-04	5.1161e-03	1.7050e-02		4.8060e-04		1.7050e-02	9.3628e-04	4.7990e-04	3.2245e-05
	N_0	236	1.651721e+11	244	443	236		244		831	1.757925e+12	242	48
	J	1.2006e+04		1.2249e+04		1.2005e+04		1.2249e+04		1.2001e+04		1.2246e+04	
	U	31.19		30.41		31.19		30.41		31.20		30.42	
	$1-\alpha$	1.000		1.000		1.000		1.000		1.000		1.000	
pwl $d(t)$	b	6.4954e-02	1.0916e+00	6.5474e-02	1.0822e+00	6.4954e-02		6.5474e-02		6.4778e-02	7.7653e-03	6.5382e-02	7.7653e-03
	d_1	8.7650e-08	3.3321e-03	1.0006e-05	3.2963e-03	1.0000e-08	4.9166e-05	1.0006e-05	4.9428e-05	8.7650e-08		1.0006e-05	
	d_2	1.8879e-04	2.2339e-03	1.8739e-04	2.2272e-03	1.8879e-04	5.8346e-05	1.8753e-04	5.8499e-05	1.8879e-04		1.8739e-04	
	d_3	6.9847e-04	5.2450e-03	7.0385e-04	5.1890e-03	6.9856e-04	2.7496e-04	7.0302e-04	2.7549e-04	6.9847e-04		7.0385e-04	
	d_4	1.2720e-03	1.3823e-02	1.2688e-03	1.3760e-02	1.2702e-03	1.5645e-03	1.2717e-03	1.5655e-03	1.2720e-03		1.2688e-03	
	N_0	253	202	257	196	253		257		254	25	257	25
	J	1.1226e+04		1.1238e+04		1.1226e+04		1.1238e+04		1.1225e+04		1.1238e+04	
	U	33.98		33.95		33.98		33.95		33.99		33.95	
	$1-\alpha$	1.000		1.000		1.000		1.000		1.000		1.000	

Table 23: **Weedy margin, no spray:** Parameter estimates μ and variance σ for Model 6 with various constraints and subsets of parameters estimated.

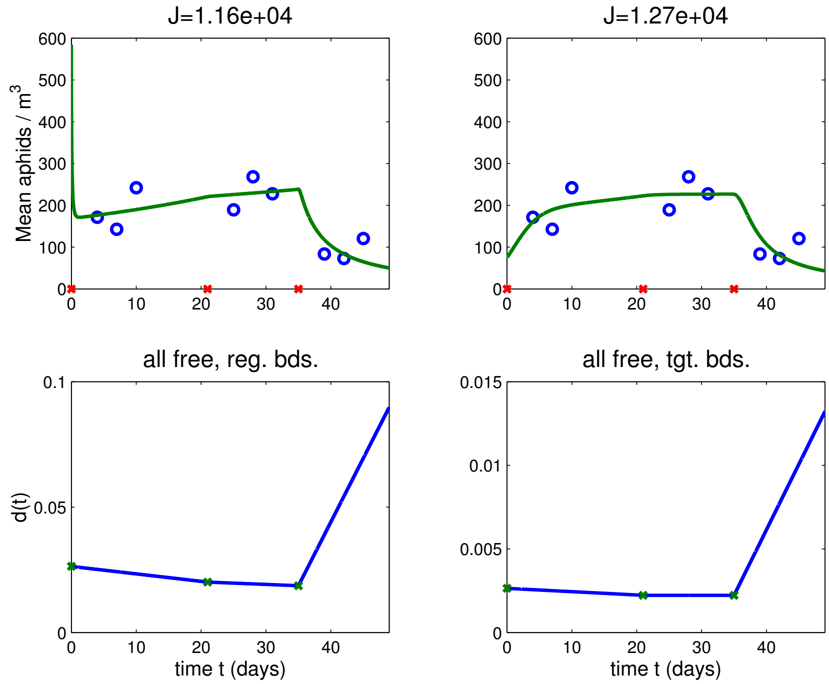

Figure 41: **Bare ground, high spray:** Comparison of Model 6 fit to data using the initial bounds (left column) and tighter bounds (right column) on the parameters. By tightening the bounds the initial condition became more reasonable and the magnitude of the death rate coefficient $d(t)$ dropped an order of magnitude.

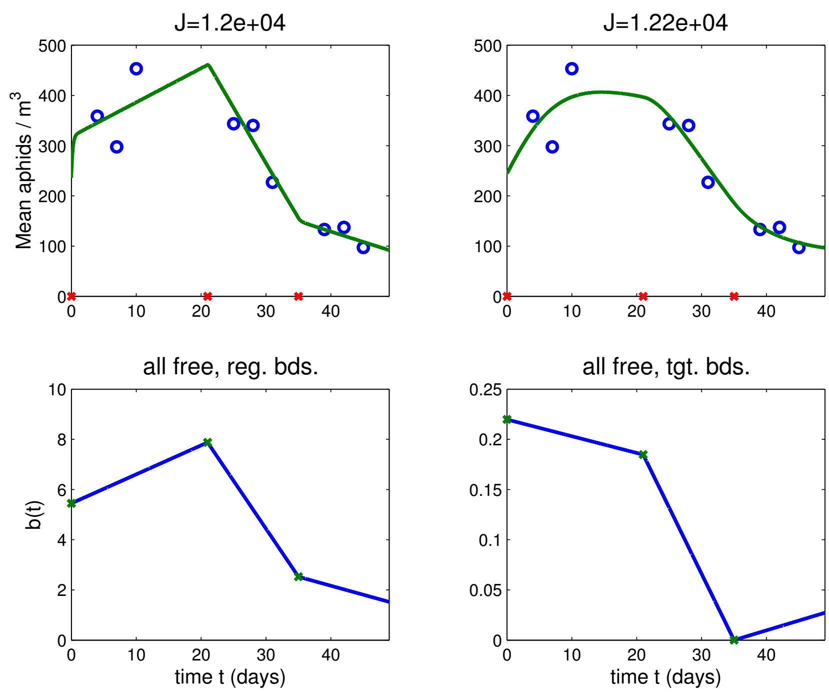

Figure 42: **Weedy ground, no spray:** Comparison of Model 6 fit to data using the initial bounds (left column) and tighter bounds (right column) on the parameters. By tightening the bounds the model fit curve smoother out considerably and the magnitude of the birth rate coefficient $b(t)$ dropped an order of magnitude.

Varying number of observations

We expect that gathering more data would substantially reduce variability of the parameter estimates. To test this hypothesis, we experimented with the number of observations (censuses) used in the experiment by using simulated data.

Simulated data were generated based taking the optimal estimated parameters for the case weedy margin, no spray, Model 3, piecewise linear coefficient $a(t)$. We consider various numbers of observations $n = 4, 6, 8, 16, 32, 64, 100$, and 500, where the observations are uniformly spaced on $[4, 45]$ days, endpoints inclusive. Note that the problem is underdetermined for the case $n = 4$ since we estimate five parameters.

Simulated exact data $\{y_i\}_{i=1}^n$ were generated using the optimal parameters in the model. We then added random normal relative noise to the data sets to get the noisy simulated data z_i: $z_i = y_i + (nl * \epsilon_i)y_i$, where ϵ_i is sampled from a $\mathcal{N}(0, 1)$ distribution and $nl = 5\%$ is the noise level.

Figure 43 shows the six of the noisy datasets considered ($n = 100, 500$ omitted), including the exact solution curve.

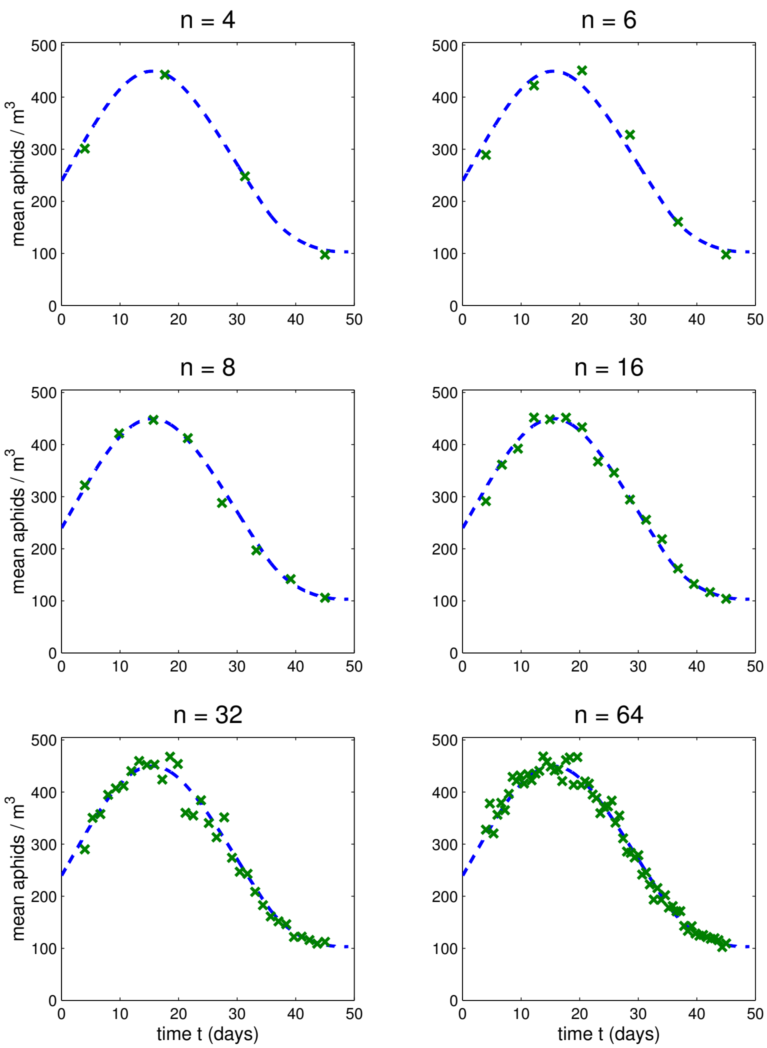

Figure 43: Simulated datasets used in variance experiment. All were generated using Model 3 at a fixed set of parameters, with $nl = 5\%$ relative random noise. Solid line denotes the exact solution and 'x' the simulated (noisy) data used.

Table 24 shows the exact and resulting estimated parameters and their standard error for each of the six cases, for both exact (clean) and noisy data. The same fitting algorithms used previously were used in these cases. Note that in the underdetermined $n = 4$ case we see imaginary values in some places due to taking the square root of a negative number. Figure 44 contains plots of the resulting fits to data for the smaller numbers of data points. In the clean data case, fits to data are essentially exact for all cases $n \geq 6$, so plots are omitted.

We have to be careful in interpreting these results since the model provides a substantially better fit to the data in these cases than to the actual data. Overall, we do not observe a monotone decreasing trend in the variance as the number of data points increases for either the clean or noisy data case, although we do see such a trend for the larger numbers of data points. This is most likely because the $\frac{1}{n-p}$ starts to dominate the standard error formula as n gets large.

	actual	$\mathbf{n=4}$		$\mathbf{n=6}$		$\mathbf{n=8}$		$\mathbf{n=16}$	
	q^*	μ	σ	μ	σ	μ	σ	μ	σ
a_1	8.1381e-02	1.1743e-02	1.5472e-03	8.0853e-02	5.7474e-04	8.1204e-02	1.0786e-04	7.9730e-02	5.2508e-04
a_2	-2.8643e-02	3.6710e-02	1.4520e-03	-2.8459e-02	3.1611e-04	-2.8582e-02	5.4810e-05	-2.8143e-02	2.4178e-04
a_3	-8.7493e-02	-2.4761e-01	3.5435e-03	-8.7692e-02	6.3710e-04	-8.7567e-02	1.1354e-04	-8.8015e-02	4.9146e-04
a_4	4.9259e-03	4.2757e-01	9.3445e-03	5.3173e-03	2.4900e-03	5.1208e-03	4.9774e-04	6.3119e-03	2.5533e-03
N_0	239	300	1.5138	240	0.85403	239	0.16626	242	0.8539
J/n		9.1499e-16		5.9907e-02		5.6628e-03		4.0087e-01	

	actual	$\mathbf{n=32}$		$\mathbf{n=64}$		$\mathbf{n=100}$		$\mathbf{n=500}$	
	q^*	μ	σ	μ	σ	μ	σ	μ	σ
a_1	8.1381e-02	7.9636e-02	3.5079e-04	7.6553e-02	6.5870e-04	7.7992e-02	3.6006e-04	7.8351e-02	1.4242e-04
a_2	-2.8643e-02	-2.8129e-02	1.5344e-04	-2.7245e-02	2.8158e-04	-2.7641e-02	1.5226e-04	-2.7785e-02	5.9413e-05
a_3	-8.7493e-02	-8.8012e-02	3.1010e-04	-8.9019e-02	5.6903e-04	-8.8591e-02	3.0724e-04	-8.8411e-02	1.1976e-04
a_4	4.9259e-03	6.5443e-03	1.7758e-03	9.3428e-03	3.4293e-03	8.4358e-03	1.8876e-03	7.9382e-03	7.5679e-04
N_0	239	242	0.58223	248	1.1266	245	0.6120	244	0.2427
J/n		3.8914e-01		2.8346e+00		1.3267e+00		1.0446e+00	

	actual	$\mathbf{n=4}$		$\mathbf{n=6}$		$\mathbf{n=8}$		$\mathbf{n=16}$	
	q^*	μ	σ	μ	σ	μ	σ	μ	σ
a_1	8.1381e-02	3.3155e-01	0 + 8.9725e-06i	8.6099e-02	2.5083e-03	8.8002e-02	1.1445e-02	1.0233e-01	7.1767e-03
a_2	-2.8643e-02	-2.5645e-01	0 + 8.4203e-06i	-1.5490e-02	1.2967e-03	-3.6776e-02	5.9307e-03	-3.4715e-02	3.2123e-03
a_3	-8.7493e-02	4.7215e-01	0 + 2.0549e-05i	-1.0577e-01	2.6417e-03	-8.2684e-02	1.2453e-02	-7.5025e-02	6.3402e-03
a_4	4.9259e-03	-1.4978e+00	0 + 5.4192e-05i	3.0935e-03	1.0864e-02	1.1543e-02	5.3646e-02	-4.9558e-02	3.4456e-02
N_0	239	100	0 + 0.0029274i	212	3	237	17	205	10
J/n		3.0781e-20		1.0545e+00		6.3982e+01		6.9975e+01	

	actual	$\mathbf{n=32}$		$\mathbf{n=64}$		$\mathbf{n=100}$		$\mathbf{n=500}$	
	q^*	μ	σ	μ	σ	μ	σ	μ	σ
a_1	8.1381e-02	9.3379e-02	1.0246e-02	7.2356e-02	5.6815e-03	7.6869e-02	4.7745e-03	8.0454e-02	2.3430e-03
a_2	-2.8643e-02	-3.3968e-02	4.4656e-03	-2.7491e-02	2.4539e-03	-2.7532e-02	2.0228e-03	-2.7955e-02	9.7500e-04
a_3	-8.7493e-02	-8.5598e-02	9.0558e-03	-9.0187e-02	4.9913e-03	-8.8683e-02	4.0842e-03	-9.0184e-02	1.9714e-03
a_4	4.9259e-03	2.1025e-02	5.0568e-02	2.3388e-02	2.9641e-02	9.1700e-03	2.5075e-02	2.3591e-02	1.2276e-02
N_0	239	220	16	260	10	248	8.1972	241	3.9389
J/n		3.1765e+02		2.1773e+02		2.3484e+02		2.8203e+02	

Table 24: Exact and estimated parameters with variance for various numbers of observations n. Top half of results are from clean (exact) datasets and bottom are from noisy.

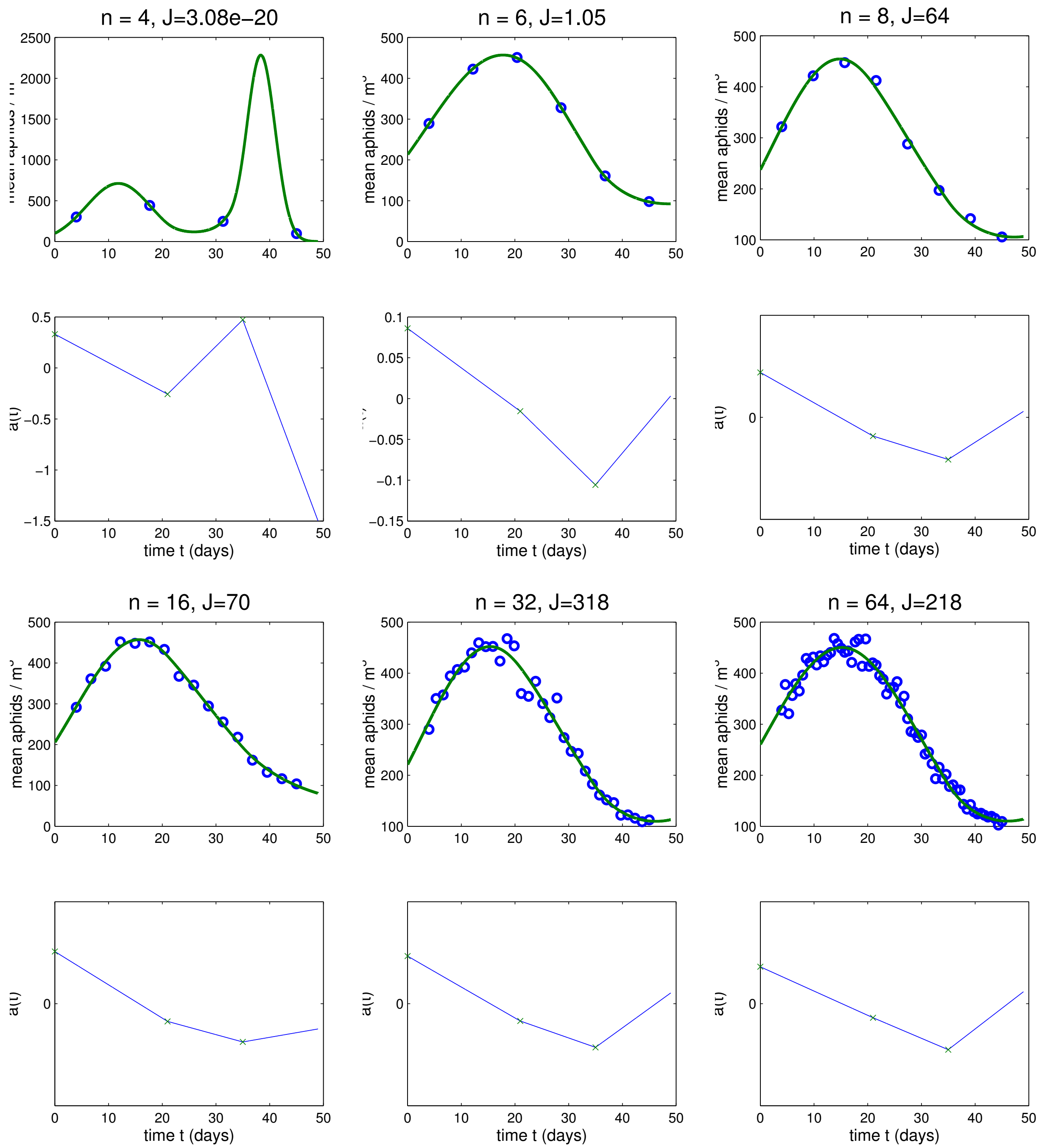

Figure 44: Resulting fits to the data with 5% noise for various values of n. Cost function values are scaled by the number of data points.

7 Summary

7.1 Time-varying coefficients

Table 25 summarizes cases in which the null hypothesis of constant coefficients in the model can be rejected at a confidence level of 75% or higher. In most cases, we do not observe a difference in the statistical significance of adding time-dependent birth coefficients $b(t)$ versus death coefficients $d(t)$, though for a few dataset/model combinations, we see statistical significance of adding $d(t)$ where adding $b(t)$ is not significant.

Model	coefficient type	Dataset					
		1	2	3	4	5	6
1	p.w. constant						
	p.w. linear						
2	p.w. constant	85.4		**98.5**	**99.9**		88.2
	p.w. linear			89.9	**99.9**		76.6
3	p.w. constant	**95.6**	77.7	**99.8**	**99.9**		**91.5**
	p.w. linear	**99.8**	82.4	**99.9**	**99.9**		**99.9**
4	p.w. constant b	**99.7**	**90.6**	**99.9**	**99.9**	**99.9**	**99.9**
	p.w. constant d	**99.7**	**92.0**	**99.9**	**99.9**	**99.9**	**99.9**
	p.w. linear b	**99.7**	78.6	**99.9**	**99.9**		**99.9**
	p.w. linear d	**99.7**	83.8	**99.9**	**99.9**		**99.9**
5	p.w. constant b			**98.2**	**95.6**	**99.9**	
	p.w. constant d			**98.9**	**96.7**	**99.9**	83.4
	p.w. linear b	**97.6**		**99.2**	**96.1**	**99.9**	
	p.w. linear d	**96.3**		**97.9**	**95.3**	**99.9**	87.3
6	p.w. constant b	**99.9**	**96.0**	**99.9**	**99.9**	**99.9**	**99.9**
	p.w. constant d	**99.9**	**98.0**	**99.9**	**99.9**	**99.9**	**99.9**
	p.w. linear b	**99.9**	88.8	**99.8**	**99.9**	**99.9**	**99.9**
	p.w. linear d	**99.9**	**94.2**	**99.9**	**99.9**	**99.9**	**99.9**
7	p.w. constant b			83.3	**93.1**		
	p.w. constant d		77.6	**99.9**	**99.9**		77.7

Table 25: Summary of statistical significance. **Bold** numbers denote confidence levels of 90% and above, while plain denote 75% to less than 90%.

However, the previous results section indicates that in many cases for the best fitting models, time-dependent parameters $d(t)$ yielded smaller least squares residuals than $b(t)$. Though these differences are slight in some cases, this finding is commensurate with the belief that the pesticide more dramatically affects the aphid death rate than the birth rate.

Overall, the results statistically justify the incorporation of time-dependent parameters in the models. There is little perceptible difference in statistical significance between adding piecewise constant versus piecewise linear coefficients. The form of these coefficients could be further refined with more information on the biological processes.

7.2 Best fitting models

We make some summary comments on which models fit the data best (in terms of least squares residual). In general, as expected, changing to models with more degrees of freedom improved the model fit to the data,

though in many cases, not appreciably. The list progresses approximately according to increasing model performance with time-varying coefficients, because their introduction yielded significantly better results.

- Model 1 is incapable of fitting our data in any situation.
- Model 2 rarely fits the data at all when taken with constant coefficients. The one exception is the data set for weedy margin, low spray, where it does a decent job in fitting the exponential trend. These can be verified by looking at the best fit curves. In some cases, improvement is made with Model 2 by using a piecewise linear time-varying parameter.
- Models 5 and 7 even taken with time-varying coefficients often were outperformed by the models listed next, also taken with time-varying coefficients.
- Model 3 with constant coefficients is really equivalent to Model 2 for our downward trend datasets and thus also does poorly fitting the data, but Model 3 with time varying coefficient $a(t)$ does a reasonable job in many cases, outperforming Models 4–7 with constant coefficients. Changing to time-varying coefficients for this model often made a statistically significant difference.
- Models 6 and 4, with their heavy decay terms, often fit the data very well when taken with time-varying coefficients. For Model 4, we often find statistically significant differences when changing to a time-varying coefficient. This is less often true, for example, with Model 5. In considering Model 6 with time-varying coefficients, we reject the null-hypothesis far more often than Model 7. In fact, we almost always find statistically significant differences when changing to a time-varying coefficient.

While Models 4 and 6 leave the smallest least squares residuals, the most general exponential Model 3 with piecewise constant or piecewise linear coefficients often yields acceptable fit to data. Its ability to fit the data combined with its simplicity make it an attractive choice for modeling. In many cases, slight improvement is made by changing to the logistic or other models, but the required extra degrees of freedom may make these models less desirable.

Our estimations for birth and death parameter values are within an order of magnitude of the values derived in the laboratory by Stark. This represents a **good fit** in general between models and experimental data, especially since it incorporates observation and process error from field data as well as the difference between the open system in the field (*in vivo*) and the closed laboratory setting (*in vitro*) in which the Stark values were derived.

7.3 Comparison between data sets

We remark that we use an ordinary least squares (OLS) data fit criterion throughout this work. OLS is equivalent to the maximum likelihood (MLE) criterion under certain assumptions on the statistical error model underlying the inverse problems. In particular, if we assume errors are independent identically distributed (i.i.d.) Gaussian with constant variance (constant across sampling), the estimation processes are equivalent.

It is common practice in population studies to use the fit criteria (cost function value) as the key quantitative metric in assessing quality of the model fit (i.e., appropriateness of the mathematical model in describing the data and biological processes). One can observe from our efforts that this is inadequate as the sole measure of success. For example, we compare Model 3 and Model 7 with constant coefficient fits to dataset 6 producing residuals of $J = 2.430 \times 10^4$ and $J = 1.627 \times 10^4$, respectively. If one considers the associated qualitative fits by comparing Figure 33 (the (3,1) entry), with Figure 35 (the (2,1) entry), it is virtually impossible to argue which is the more appropriate model. However, we note that in Model 3, adding degrees of freedom by moving to a time-dependent coefficient, yields statistically significant improvement at the $p < 0.1$ level whether we use piecewise constant or piecewise linear coefficients. The corresponding

analysis with Model 7 reveals that allowing piecewise constant coefficients does not result in a statistically significant improvement in the fit. Since one might expect that from a biological perspective, time varying rates are important in these data, one would be more likely to favor Model 3 over Model 7 even though the residual for Model 7 with constant coefficients is smaller than that for the comparable Model 3. This subjective analysis illustrates how difficult it is in general to combine strictly analytical results from model fitting with biological understanding and expectations in drawing conclusions about the "best" model for a given experimental data set.

Nonetheless, the ultimate goal of this model fitting is to make comparisons between the various margin and spray combinations explored in the field study. Therefore we present an example comparison and analysis which offers promise in the difficult task of drawing biological implications from the model fitting results detailed previously. The simplicity and biological plausibility of the basic exponential model (Model 3) and logistic model (Model 6) make them good candidates for these comparisons. Here we consider the case of piecewise linear coefficients, since they probably better reflect the dynamics of selective pesticide spray.

In Figure 45 (left panel), we plot differences $\delta_a(t)$ in time-varying birth/death rates for bare margins versus weedy margins ($\delta_a(t) = a_{\text{bare}}(t) - a_{\text{weedy}}(t)$), for Model 3. In the right panel, we plot differences $\delta_d(t)$ in time-varying death rates ($\delta_d(t) = d_{\text{bare}}(t) - d_{\text{weedy}}(t)$) for Model 6. In previous efforts, Banks [5] investigated the difference in aphid densities in plots with bare margin and those with weedy margins, finding a four- to five-fold increase in densities for bare margin plots over those for weedy margin plots. These findings suggested a strong interaction between margin type and aphid densities, perhaps due to predation differences for differing margin types (at least when analyzing static (in time) datasets). The current experiments involve time series data and invite the question of interaction of different margin types with pesticide levels as manifested in birth/death rates over time.

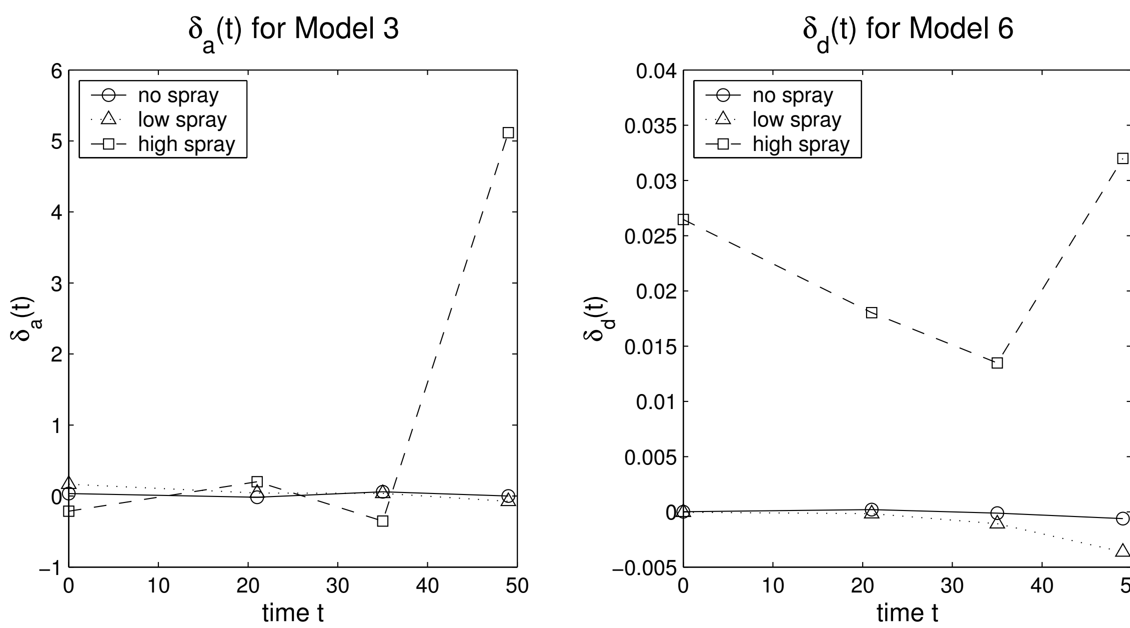

Figure 45: Plot of difference due to margin type in time-varying coefficients for Model 3 and Model 6.

The analysis depicted in Figure 45 reveals that for no spray or light spray pesticide treatments, habitat margin type has little effect on aphid birth/death rates. However for high levels of spray, there is a marked difference between rates over time as a function of margin type. In particular, one can use the information embodied in Figure 45 to argue that weedy margin habitats produce increasingly lower cumulative growth

rates with time during the duration of the high spray experiments. This suggests a strong interaction between margin type (possibly the pressure of predators) and pesticide spray level, whose synergism affects aphid density decrease in the case of sufficiently high pesticide levels. This interaction is also supported statistically by the MANOVA results detailed in [6].

A potentially more valuable comparison of Models 3 and 6 can be made by instead comparing $a(t)$ for Model 3 to its counterpart in Model 6: $b - d(t)N(t)$. This is more representative of the instantaneous growth rate in the latter model. Figure 46 contains plots of the time-varying model coefficients for Models 3 and 6. We observe that the average rates predicted by Model 3 are similar in most cases to those predicted by Model 6, with exceptions where extreme coefficients were predicted. In several cases, the time series trends are comparable as well.

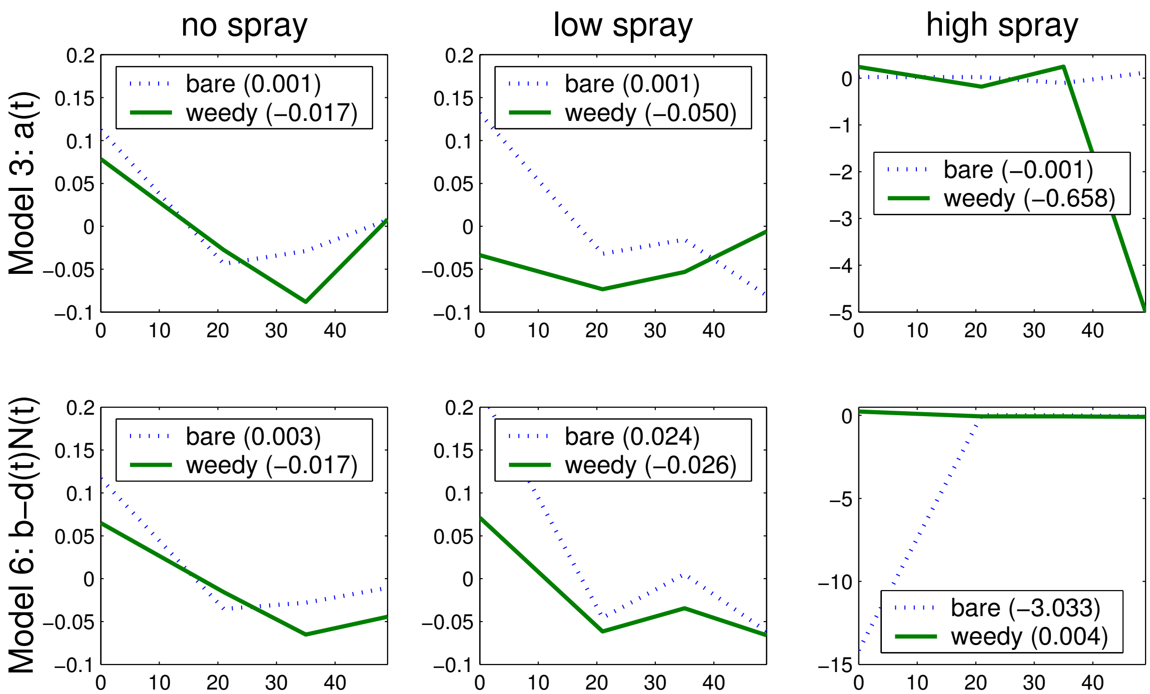

Figure 46: Plot of time-varying coefficients for Model 3 (top row) and Model 6 (bottom row). Graph legends are annotated with the average growth rate over the time period considered. Observe similarities between the rates in the separate models.

Finally, we examine Figure 47, which is comparable to the graphs in Figure 45 above, but contains plots of the difference in $b - d(t)N(t)$ between bare and weedy ground for only the last three intervals. Again there is evidence of the substantial difference in growth rates between bare and weedy ground as one changes spray concentration, with the greatest difference occurring at high spray levels.

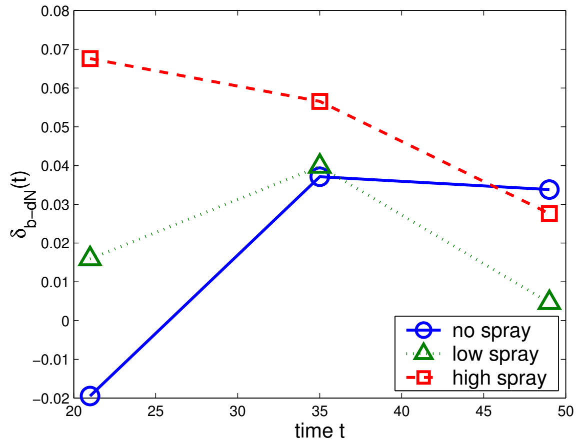

Figure 47: Plot of difference due to margin type in time-varying coefficients for Model 6. Difference plotted is for the bare growth rate minus the weedy growth rate using $b - d(t)N(t)$ as the rate.

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